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# Crustacea Decapoda Crangonidae : Revision of the three closely related genera Aegaeon Agassiz, 1846, Pontocaris Bate, 1888 and Parapontocaris Alcock, 1901

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#### ABSTRACT

The species of *Pontocaris* Bate, 1888, and related genera, *Aegaeon* Agassiz, 1846 and *Parapontocaris* Alcock, 1901, are reviewed based on the abundant samples collected by ORSTOM (Institut français de Recherche scientifique pour le Développement en Coopération), the Muséum national d'Histoire naturelle, the Forschungsinstitut Senckenberg, and the National Taiwan Ocean University, as well as those deposited at other museums and institutions.

Altogether 21 species and one subspecies are recognized which appear to form three natural groups. The genus *Parapontocaris* Alcock, 1901 is retained for the 6 species assigned to it by CHACE (1984), but different characters are used to differentiate them.

An interlocking mechanism between the posterior thoracic sternites and the carapace is found in all species of the *Pontocaris propensalata* group, but not in the others. Furthermore, females of this group can modify their pereiopods, probably for the care of the eggs, when they molt for spawning. Such modification of the pereiopods is unique in the carideans according to present knowledge. Thus, the genus *Pontocaris* Bate, 1888, is now restricted to the species of this group and BRUCE's (1988) *Pontocheras* becomes a junior synonym of the former. At present 10 species and one subspecies are recognized in this group, with the names *P. affinis* (Alcock, 1901) and *P. hilarula* (de Man, 1918) revived and four new species and one new subspecies described : *P. major* from the Philippines, *P. laurentae* and *P. spinifera* from Indonesia, *P. profundior* from the Red Sea and Gulf of Aden, and *P. affinis allodactylus* from the Red Sea.

The name Aegaeon Agassiz, 1846 is revived for five species with characters intermediate between Parapontocaris and Pontocaris (as defined here), namely A. cataphractus (Olivi, 1792), A. lacazei (Gourret, 1887), A. orientalis Henderson, 1893, A. rathbuni de Man, 1918 and A. boschii (Christoffersen, 1988).

Keys for distinguishing these three genera and the identification of the species are provided. The distribution and evolution, as well as sexual dimorphism and polymorphism in females, of these species are briefly discussed. Both the morphological characters and distribution patterns suggest that the genus *Parapontocaris* is relatively more ancient and has a typical Tethys distribution. On the other hand, species of *Pontocaris* possess many advanced characters and are still actively evolving in the Indo-West Pacific. The intermediate genus *Aegaeon* probably forms a link between the above two genera and has successfully invaded the Atlantic from the original Indo-West Pacific distribution.

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### RÉSUMÉ

## Crustacea Decapoda Crangonidae : Révision des trois genres voisins Aegaeon Agassiz, 1846, Pontocaris Bate, 1888, et Parapontocaris Alcock, 1901.

Les espèces du genre *Pontocaris* Bate, 1888, et des genres voisins sont réexaminées en se basant sur l'abondant matériel récolté par l'ORSTOM (Institut français de Recherche scientifique pour le Développement en Coopération), le Muséum national d'Histoire naturelle, le Forschungsinstitut Senckenberg, et la National Taiwan Ocean University, ainsi que plusieurs autres provenant de divers Muséums et Instituts.

En tout 21 espèces et une sous-espèce sont reconnues; elles semblent former trois groupes naturels.

Le genre Parapontocaris Alcock, 1901, est conservé pour les six espèces assignées à ce genre par CHACE (1984) mais des caractères différents de ceux utilisés par CHACE pour les distinguer sont utilisés.

Un mécanisme de blocage entre les sternites thoraciques postérieurs et la carapace est observé chez *Pontocaris* propensalata Bate, 1888, et les espèces voisines qui forment ainsi un groupe propensalata. Un tel mécanisme n'est pas observé chez les autres espèces. De plus, les femelles du groupe propensalata présentent une modification de leurs péréiopodes, probablement pour mieux prendre soins de leurs œufs, lors de la mue précédant la ponte. Une telle modification des péréiopodes semble unique chez les Carides, sur la base de nos connaissances actuelles. En conséquence le genre *Pontocaris* Bate, 1888, est réduit aux espèces du groupe propensalata et le genre Pontocheras de BRUCE est mis en synonymie avec lui. Actuellement 10 espèces et une sous-espèce sont reconnues dans ce genre. *Pontocaris affinis* (Alcock, 1901) et *P. hilarula* (de Man, 1918) sont ressucitées, tandis que quatre espèces et une sous-espèce sont décrites : *P. major* des Philippines, *P. laurentae* et *P. spinifera* d'Indonésie, *P. profundior* de la mer Rouge et du golfe d'Aden, et *P. affinis allodactylus* de la mer Rouge.

Le nom Aegaeon Agassiz, 1846, est ressuscité pour les cinq autres espèces : A. cataphractus (Olivi, 1792), A. lacazei (Gourret, 1887), A. orientalis Henderson, 1893, A. rathbuni de Man, 1918 et A. boschii (Christoffersen, 1988). Il possède des caractères intermédiaires entre Parapontocaris et Pontocaris, tels que nous les avons définis ici.

Des clés permettant de distinguer ces trois genres et d'identifier les espèces sont proposées. La distribution et l'évolution de ces espèces, aussi bien que le dimorphisme sexuel et le polymorphisme chez les femelles, sont brièvement discutés. Les caractères morphologiques et les distributions suggèrent que le genre *Parapontocaris* est relativement plus ancien et a une distribution typiquement téthysienne. D'un autre côté, les espèces du genre *Pontocaris* possèdent de nombreux caractères évolués et sont encore en pleine évolution dans l'Indo-ouest Pacifique. Le genre intermédiaire *Aegaeon* forme probablement un maillon entre les deux genres précédents et a envahi l'Atlantique à partir de l'Indo-ouest Pacifique.

#### INTRODUCTION

The present paper provides a revision of the three genera, that before 1984, were thought to be a single genus, named *Pontocaris* or *Egeon* (or its variant spelling *Aegeon*). This revision was made possible because I had at my disposal not only an important material from Taiwanese waters (National Taiwan Ocean University, Keelung - NTOU), but also the very extensive collections made by the MUSORSTOM expeditions in the Philippines, Indonesia and New Caledonia. Furthermore, much material from other sources present in the collection of the Muséum national d'Histoire naturelle in Paris (MNHN) could be consulted as well as specimens from other institutions : Nationaal Natuurhistorisch Museum, Leiden (RMNH); Forschungsinstitut Senckenberg, Frankfurt (SMF); Zoologisches Sammlung des Bayerischen Staates, Munchen (ZSM); Zoologisch Museum, University of Amsterdam, Amsterdam (ZMA); National Museum of Natural History, Washington, D.C. (USNM); The Natural History Museum, London (NHM); University Museum of Zoology, Cambridge (UMZC); Shimonoseki University of Fisheries, Shimonoseki (SUF); Northern Territory Museum of Arts and Sciences, Darwin (NTM); and Universidade Federal da Paraíba, Paraíba (UFPB).

The first generic name given to this group was *Egeon* Bosc, 1813, and this name (or its incorrect subsequent spelling *Aegeon* Kinahan, 1861) was generally used for it until 1947, when it was shown that *Egeon* Bosc, 1813, is invalid as it is a junior homonym of *Egeon* de Montfort, 1808, a genus of Mollusca (see HOLTHUIS, 1947). The name *Aegeon* Kinahan, 1861, cannot be used for the genus as it is an incorrect spelling and therefore an unavailable name (International Code of Zoological Nomenclature, Art. 19a). As in 1947, *Pontocaris* Bate, 1888, and *Parapontocaris* Alcock, 1901, were considered junior synonyms of *Egeon* Bosc, the senior name *Pontocaris* was used to replace *Egeon*. In 1984, CHACE showed that *Pontocaris* and *Parapontocaris* are different genera and

reinstated the latter. In 1947, HOLTHUIS had overlooked the fact that AGASSIZ, 1846, had published the emendation *Aegaeon* for *Egeon* Bosc. As an emendation is an available name (Art. 19a) it should have priority over *Pontocaris* as a replacement name for *Egeon*. A difficulty here is that AGASSIZ, 1846, also emended *Egeon* de Montfort, 1808, to *Aegaeon*. There are thus two simultaneously published names *Aegaeon* Agassiz, 1846, one for a crustacean genus and one for a genus of Mollusca; so it is up to the first reviser (see Code Art. 24a) to select one of these names and give it precedence over the other. In the present case the first reviser is HOLTHUIS (1993) who gave *Aegaeon* Agassiz, 1846 precedence over the same name for the molluscan genus. This action is fortunate, in so far as it provides a name for the genus of which *Cancer cataphractus* Olivi, 1792 is the type, and which in the present paper is shown to be distinct from the genus *Pontocaris* which has *Pontocaris propensalata* Bate, 1888 as type. Thus the three genera in which the old *Egeon* is split up here, all have an available published name : *Aegaeon* Agassiz, 1846, *Pontocaris* Bate, 1888 and *Parapontocaris* Alcock, 1901.

CHACE (1984), who was the first to recognize *Parapontocaris* as a genus distinct from *Pontocaris* assigned 6 species to the former genus, 7 to the latter. These 13 species are also recognized here (4 in *Aegaeon*, 3 in *Pontocaris* and 6 in *Parapontocaris*). One more species, *Pontocaris boschii* Christoffersen, 1988, described after CHACE's (1984) revision, is here assigned to *Aegaeon*. The number of *Parapontocaris* species remains the same as recognized by CHACE in 1984. Of *Pontocaris*, however, 7 more species are recognized here than in 1984 : (a) two of these, namely *P. affinis* (Alcock, 1901) and *P. hilarula* (de Man, 1918), had been incorrectly synonymized with other species; (b) one (*Pontocheras arafurae* Bruce, 1988) was described after 1984 and was placed in a new genus; and (c) four species and a subspecies are described here as new (*P. laurentae*, *P. major*, *P. profundior*, *P. spinifera* and *P. affinis allodactylus*). The keys given here differ somewhat from those provided by CHACE (1984) as the emphasis is placed on different characters.

The type species of the genus *Pontocheras* established by BRUCE, 1988, proves to be a true *Pontocaris*, so that *Pontocheras* has to be placed in the synonymy of *Pontocaris*, but the species *Pontocheras arafurae* [now *Pontocaris arafurae* (Bruce)] proves to be a good species.

The three genera recognized here can be distinguished with the help of the following key :

- Carapace with 7 or more dorsal teeth and lateral carina III continuous with pterygostomian spine; branchiostegal spine extraordinarily large and usually exceeding 2/3 of outer margin of laterally extended scaphocerite; thoracic sternites interlocked with posteroventral border of carapace; pereiopods II and/or V modified when females molt for spawning; telson devoid of spines \_\_\_\_\_\_\_ Pontocaris \_\_\_\_\_\_\_ Pontocaris \_\_\_\_\_\_\_ Carapace with less than 6 dorsal teeth and lateral carina III continuous with branchiostegal spine; branchiostegal spine generally reaching less than half of outer margin of laterally extended scaphocerite; thoracic sternites not interlocked with ventral carapace; pereiopods not particularly modified when females molt for spawning; telson with dorsolateral and/or terminal spines \_\_\_\_\_\_ 2
- Rostrum pointed and armed with 2 pairs of lateral teeth; lateral carina I on carapace generally having less than 6 teeth; abdominal sternites unarmed medially ... Parapontocaris

The colorations of these species appear to be similarly dull and without particular markings. Nevertheless, certain peculiar characteristics, such as the interlocking of the thoracic sternum with the carapace and the modification of the pereiopods of females when they molt to spawn, are found in the species of *Pontocaris*. The latter characteristic is also likely to be unique in the carideans as far as known from present knowledge.

Although having the fewest species, the genus Aegaeon has the widest geographical distribution, from the Indo-West-Pacific to the Atlantic (fig. 19), and occurs at 12 m to at least 809 m depth. Species of Parapontocaris

all come from more than 200 m depth and are found in the Indo-West Pacific and the Caribbean (fig. 21). The species of *Pontocaris* are only recorded in the Indo-West Pacific, with the highest concentration in the Indo-Malay region (fig. 20). Nevertheless, the vertical distribution of *Pontocaris* is very wide and a new species from the Red Sea even occurs in waters at more than 1400 m depth. A brief discussion on the distribution and evolution of these three genera is provided.

Other than the usual sexual dimorphisms of the pleopods and the outer antennular flagella of males being much thicker than those of the females, marked polymorphism in the females of these three genera is found between those at the spawning molt and those not. The body of the males and young specimens are generally more slender (also see CHACE, 1984) and with the sculpture rather obscure or less developed (also see FUJINO & MIYAKE, 1970). Adult females are rather similar to males, but when they molt for spawning their abdominal sternites and pleura (particularly those of somite II) are distinctly broadened, the pleopods become heavily setose, the posterior two thoracic sternites are widened and the median carinae are leveled or faint. In the species of *Pontocaris* and *Parapontocaris*, a pair of ventrally directed teeth is present at thoracic sternite VIII behind the coxae of the last pereiopod. However, this pair of teeth is absent in females that have molted for spawning. The functions of this pair of teeth and the median carinae at the posterior thoracic sternites are probably related to copulation by preventing the attachment of spermatophores to females that are not ready to spawn. Furthermore, as mentioned above, the females of *Pontocaris* can even modify their pereiopods II and/or V when they molt for spawning.

Possible polymorphisms or developmental changes at the thoracic and abdominal sternites in crangonid females have been noticed by many authors (eg. BATE, 1888; DE MAN, 1920; CHRISTOFFERSEN, 1988; DURIS, 1992). However, most workers did not have enough material to investigate this subject further. The abundant material in the present study reveals that the differences of the thoracic and abdominal sternites are only part of the marked polymorphisms exhibited in many crangonids between females molted for spawning and those not yet prepared to spawn. For convenience, females at the spawning molt are referred here as "spawning females" while the term "non-spawning females" is used for those that are not at the spawning molt. It should be noticed that, other than those carrying eggs, spawning females also include those that have not yet laid eggs and those with the eggs just hatched. Furthermore, non-spawning females are not necessary smaller than spawning females. For example, in *P. sibogae* (de Man, 1918) the largest non-spawning female is cl 12.6 mm, while the size of spawning females is from cl 9.9 mm to 14.8 mm. Thus, even though both are adult females, the differences described by DE MAN (1920) in the posterior thoracic sternites between the types of *Aegeon sibogae* and *Aegeon sibogae* var. *intermedia* actually represent the general differences between the spawning and non-spawning females in these genera.

The measurements given are carapacial length (cl) which refers to the postorbital carapacial length. The length of the outer margin of the scaphocerite is measured from the outer base of the scaphocerite to the tip of the distolateral spine. The terminology for the various body parts used in the text is indicated in fig. 1.

In the lists of material examined the capital letters preceding the station number refer to the gear used: DC: Charcot dredge, DW: Waren dredge, CP: Beam trawl, CC: Otter trawl (shrimps).

The research and fishing vessels' names are in italics, between inverted commas.

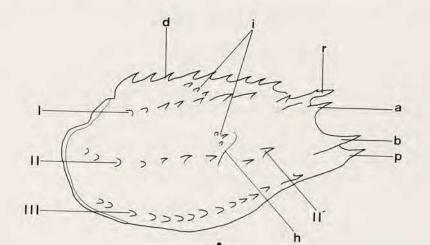
FIG. 1. - Terminology used for the different body parts in the present study.

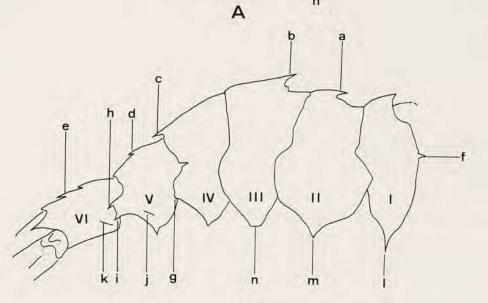
A - Lateral carapace. d : dorsal carina, I : lateral carina I, II : posterior part of lateral carina II, II : anterior part of lateral carina II, III : lateral carina III, r : rostrum, a : antennal spine, b : branchiostegal spine, p : pterygostomian spine, i : intermediate tubercles, h : hepatic groove.

B - Lateral abdomen. a : dorsal tooth of tergite II, b : anterodorsal tooth of tergite III, c : posteromedian spine of tergite IV, d : dorsolateral spines of tergite V, e : dorsolateral spines of tergite VI, f : anterobasal spine of pleuron I, g : posterodistal tubercle of pleuron IV, h : posterobasal spine of pleuron V, i : posterodistal spine of pleuron V, j : posterior oblique ridge of pleuron V, k : anteroventral ridge of somite VI, l : ventral margin elongate and acute, m : ventral margin pointed or subacute, n : ventral margin truncate.

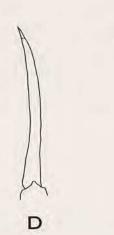
C - Dorsal view of abdominal tergites I to III. d : dorsal carina, c : lateral ridges continuous, i : lateral ridges interrupted.

**D** - Dactylus of pereiopod V simple. — **D**': Dactylus of pereiopod V modified. **1**: distal end lamella, **s**: disto-outer spine, **f**: disto-outer flap or hood.

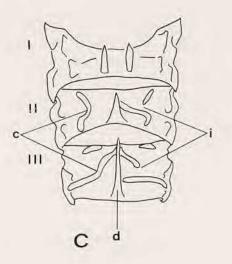




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### SYSTEMATIC ACCOUNT

#### Aegaeon Agassiz, 1846

*Egeon* Bosc, 1813 : 233 [Gender : masculine, type-species : *Cancer cataphractus* Olivi, 1792]. — RISSO, 1816 : 99; 1827 : 64. — DESMAREST, 1825 : 218. — GUÉRIN MÉNEVILLE, 1832 : 40;. — STEBBING, 1893 : 226.

Aegaeon Agassiz, 1846: 134 [Gender : masculine, type-species : Cancer cataphractus Olivi, 1792]. — HOLTHUIS, 1993 : 285.

Aegeon - Kinahan, 1861: 24. — Carus, 1885: 483. — Ortmann, 1890: 530. — Stebbing, 1900: 49; 1910: 383. —
 Alcock, 1901: 117. — Kemp, 1910a: 155; 1916: 374. — Balss, 1914a: 70. — De Man, 1920: 290. — Boone, 1927: 124. — Barnard, 1950: 811.

Aegon - POIZAT, 1969 : 396.

DIAGNOSIS. — Body slender to robust. Rostrum short and bifurcate or tridentate, with one pair of small and sometimes inconspicuous lateral spines near base. Carapace 1.05-1.7 times as long as broad, usually with four or five dorsal teeth; lateral carina I bearing 6-9 teeth, anteriormost tooth may be separated from other teeth; lateral carina II with 6-11 teeth and lateral carina III having 4-16 teeth; anterior end of lateral carina III and sometimes also that of lateral carina II continuous with branchiostegal spine. Hepatic groove rudimentary to distinct. Branchiostegal spine not particularly large and generally extending to less than half way along outer margin of laterally extended scaphocerite. Pterygostomian spine moderately to much smaller than antennal spine. Scaphocerite narrow to broad; from 1.25 to 2.22 times as long as wide, with distolateral tooth as large as or smaller than antennal spine and more or less to far exceeding distal margin of lamella. Thoracic sternum not interlocked with posteroventral carapace. Pereiopod V without distinct ventral tooth behind coxa and pereiopods not modified in females at spawning molt. Abdominal integument with regularly or irregularly arranged ridges and sometimes also lobes or squamae. Abdominal sternites armed with distinct median spines, at least in males. Abdominal pleura more or less triangular or truncate, ventral margins never acute. Telson with 1-2 pairs of dorsolateral spines and 0-3 pairs of terminal spines.

DISTRIBUTION. - World-wide tropical and temperate seas except eastern Pacific. At depths of 12-809 m.

REMARKS. — The present genus is revived mainly to accommodate those species with characters intermediate between the *P. propensalata* and *P. bengalensis* (Wood-Mason & Alcock, 1891) groups. They differ significantly from the former group in that the posterior thoracic sternites are not locked with the posteroventral border of the carapace, and the pereiopods are not modified in females at spawning molt. On the other hand, the degenerated apex of the rostrum, the presence of distinct median spines (at least in males) on the abdominal sternites and the constantly greater number of teeth in the lateral carapacial carina I seem to be sufficient justification for setting them apart from the rather homogeneous *P. bengalensis* group. Although the characters used here in defining the present genus are somewhat arbitrary, its establishment may emphasize its intermediate position or perhaps mark it as a convincing link between the *P. propensalata* and *P. bengalensis* groups. Since the names *Pontocaris* and *Parapontocaris* should be used for the *P. propensalata* and *P. bengalensis* groups, respectively (through the selections of the type-species of these two genera by HOLTHUIS, 1947, 1955), another generic name is needed for the intermediate group. The old name *Aegaeon* Agassiz, 1846, with *Cancer cataphractus* Olivi, 1792, as the typespecies, is available as a result of treating *Aegaeon* Agassiz, the replacement name for *Egeon* Bosc, 1813, as having precedence over *Aegaeon* Agassiz (the replacement name of *Egeon* de Montfort, 1808), and is revived here for this group (see HOLTHUIS, 1993).

At present five species are recognized in this genus, with *Pontocaris habereri* Doflein, 1902 and *Aegeon rugulosum* Borradaile, 1915 being treated as junior synonyms of *A. lacazei* (Gourret, 1887) and *A. orientalis* Henderson, 1893, respectively. The re-examination of CHRISTOFFERSEN's (1988) *Pontocaris boschii* from the western Atlantic shows that this species belongs to *Aegaeon* instead of *Pontocaris*, by the present definitions. Amongst these five rather heterogeneous species, *A. cataphractus* and *A. lacazei* are more closely related to *Pontocaris* by the presence of a distinct hepatic groove, the anterior of the lateral carapacial carina II on the same level with the branchiostegal spine and the abdominal sculpturing composed of lobes in addition to ridges and

carinae. Besides lacking a distinct hepatic groove, the tridentate rostrum of *A. boschii* and *A. orientalis*, and the abdominal sculpturing of *A. rathbuni* de Man, 1918, resemble those of the species of *Parapontocaris*. Nevertheless, the slender body and narrow scaphocerite of *A. lacazei* also show some similarities with *Parapontocaris* while the broadened body and scaphocerite align *A. orientalis* with *Pontocaris*.

Although distinct median spines are always present on the abdominal sternites in the males, only median tubercles are present on the abdominal sternites in the females of *A. orientalis* and *A. boschii*. Moreover, in the females of *A. lacazei* and *A. rathbuni*, the median spines on the posterior abdominal sternites are also reduced to tubercles (on last two sternites in the former and on the last three sternites in the latter, but median spines on the abdominal sternites I and II larger in *A. rathbuni* females than in *A. lacazei* females). Only in *A. cataphractus* are strong median spines retained in females (only slightly smaller than those of males). Contrary to the other two genera, there is no distinct ventral tooth behind the coxa of the last pereiopod, though a minute spine (fused with the coxa) is sometimes present in males. The median carinae on the posterior thoracic sternites, however, are also eroded or become faint in spawning females of this genus.

Although only five species are known, the present genus has a very wide geographical and vertical distribution. Three species, namely *A. cataphractus*, *A. orientalis* and *A. boschii*, mainly occur in shallow waters, while *A. lacazei* and *A. rathbuni* are found in deeper waters. Four species occur in the Indo-West Pacific, with two of them also found in the Mediterranean and East Atlantic. On the other hand, one representative of this genus has recently been recorded from the southwestern Atlantic. It is interesting that the most widely distributed species, *A. lacazei*, has also been found in the temperate waters of Ireland and New Zealand.

## Key to the species of the genus Aegaeon

1. Hepatic groove distinct; anterior end of lateral carina II of carapace on same level as branchiostegal spine; abdominal somite VI usually bearing 2 pairs of dorsolateral spines
<ul> <li>Hepatic groove rudimentary; anterior end of lateral carina II of carapace not on same level as branchiostegal spine; abdominal somite VI bearing 1 pair of dorsolateral spines 3</li> </ul>
<ul> <li>2. Tubercles present between dorsal carina and lateral carina I of carapace; abdominal tergite II lacking dorsal spine, but with lateral ridges continuous</li></ul>
<ul> <li>3. Rostrum bifurcate; lateral ridges on abdominal tergites II and III almost straight</li></ul>
4. Carapace having 5 dorsal teeth; anteriormost tooth of lateral carapacial carina I of similar size and not particularly separated from other teeth of the carina; abdominal pleuron V lacking posterobasal spine and lateral surfaces of abdominal somite VI without anteroventral ridge
— Carapace having 4 dorsal teeth; anteriormost tooth of lateral carapacial carina I minute and well separated from other teeth of the carina; abdominal pleuron V bearing posterobasal spine and lateral surfaces of abdominal somite VI having anteroventral ridge 

#### Aegaeon cataphractus (Olivi, 1792)

#### Fig. 2

Cancer cataphractus Olivi, 1792 : 50, pl. 3 fig. 1 (type-locality : Adriatic sea). — WHITE, 1847 : 74.
 Egeon loricatus Risso, 1816 : 100 (type-locality : Nice); 1827 : 58, pl. 1 fig. 3. — DESMAREST, 1825 : 219. — ROUX, 1831 : 34.

Crangon catapractus - H. MILNE EDWARDS, 1837 : 343; 1839, pl. 51, fig. 3. - LUCAS, 1849 : 39.

Crangon cataphractus - HELLER, 1863: 230, pl. 7, figs 12-15. — NARDO, 1869: 237. — CARUS, 1885: 482.

Crangon (Cheraphilus) cataphractus - MIERS, 1881 : 365.

Aegeon cataphractus - Ortmann, 1890: 535. — Stebbing, 1900: 50; 1910: 383. — Pearson, 1905: 89. — Pesta, 1912: 103. — Balss, 1916: 31. — Kemp, 1916: 375. — Monod, 1933: 465. — Calman, 1939: 222. — Barnard, 1950: 812, fig. 154.

Pontophilus cataphractus - ORTMANN, 1895 : 183. - RATHBUN, 1900 : 311.

Aegeon cataphracta - DE MAN, 1920 : 292.

Pontocaris cataphracta - HOLTHUIS, 1949: 254; 1951: 153. — KENSLEY, 1981: 28. — CHACE, 1984: 42.

Pontocaris cataphractus - KENSLEY, 1969: 155; 1972: 64, fig. 30v. - HOLTHUIS, 1987: 214, fig. 2.

Not Aegeon cataphractus - BORRADAILE, 1916 : 90 [= A. lacazei (Gourret, 1887)].

MATERIAL EXAMINED. — Mediterranean Sea. Nice, "Travailleur", 1882 : 1  $\Im$  7.9 mm (MNHN-Na 10749). — Golfe d'Ajaccio, "Melita", stn 69-96, 50 m, 30.7.1891 : 3  $\mathring{\sigma}$  6.6-7.6 mm; 3 ovig.  $\Im$  8.6-10.9 mm; 1  $\Im$  8.2 mm (MNHN-Na 1179). — Alger : 1  $\mathring{\sigma}$  6.2 mm; 1  $\Im$  10.0 mm (MNHN-Na 1178). — Tunisia (north of Djerba), "Thalassa": stn V451, 34°06.7'N, 11°06.7'E, 51-60 m, 27.11.1969 : 1  $\mathring{\sigma}$  6.6 mm; 1  $\Im$  9.5 mm (NTOU, MNHN-Na 10392 in exchange). — Stn V463, 34°03.4'N, 11°06.4'E, 52-57 m, 29.11.1969 : 1  $\Im$  9.1 mm (MNHN-Na 10393).

**Spain**. "Talisman" : stn 5, Gulf of Cádiz, 36°26'N, 6°27'W, 60 m, 9.6.1883 : 1 ♂ 7.2 mm; 1 ovig. ♀ 11.0 mm; 1 ♀ 10.9 mm (MNHN-Na 4309).

**Ghana**. Guinean Trawling Survey, "La Rafale", Guinean 1, trans. 30, stn 3, 30 m, 21.9.1963 : 1 \overline 5.5 mm (MNHN-Na 8046).

Cameroon. "Ombango" : stn CH 46, 3°50'N, 9°5'E, 48 m, mud, 24.8.1963 : 3 ♀ 8.8-10.5 mm (MNHN-Na 7784). — Stn CH 51, 3°54'30"N, 8°53'E, 62-64 m, mud, 26.8.1963 : 2 ovig. ♀ 9.9-11.7 mm; 5 ♀ 9.4-11.2 mm (MNHN-Na 7783).

**Congo**. Au large de Pte-Noire, "*Ombango*" : stn 419, 50 m, 4.5.1962 : 1 8.3 mm (MNHN-Na 7785). — 4°42'S, 11°35'E, 50 m, 12.8.1966 : 1 10.2 mm (MNHN-Na 7786).

**Madagascar**. "Vauban" : stn 72, 25°11.2'S, 47°14.7'E, 85-90 m, 3.3.1973 : 6 ♀ 5.7-10.2 mm (MNHN). — Stn 80, 25°2.7'S, 47°5.8'E, 65-70 m, 4.3.1973 : 5 ♂ 6.5-7.0 mm; 1 ovig. ♀ 9.3 mm; 12 ♀ 4.7-9.7 mm (MNHN). — Stn 130, 15°20'S, 46°11.5'E, 170-175 m, 19.1.1975 : 1 ♀ 12.0 mm (MNHN).

Gulf of Aden. "Meteor", cruise 5, leg 2, stn 283, beamtrawl, 12°30.9'N, 44°47.7'E, 76 m, 16.3.1987 : 4 spec. (SMF).

Red Sea. Gulf of Aquaba, Eilath : stn 7, 37-49 m, 6.4.1966 : 1 spec. (RMNH-D42370). — Stn 8, 62-80 m, 7.4.1966 : 1 spec. (RMNH-D42371).

DIAGNOSIS. - Body robust and integument hard. Rostrum bifurcate. Carapace about 1.1 (1.04-1.26) times as long as broad; dorsal carina armed with 4 teeth; lateral carina I bearing 6-8 teeth anteriormost tooth distinctly separated from other teeth; in-between dorsal carina and lateral carina I 4-8 teeth or tubercles arranged in "V" near mid-carapace and three other small tubercles placed in triangular format in front of dorsal carina; lateral carina II interrupted by strong hepatic groove, anterior part bearing one tooth, posterior part with 5-7 teeth; in-between lateral carinae I and II two or three (rarely one) denticles present at hepatic groove; lateral carina III provided with 10-15 (mostly 10-13) teeth behind branchiostegal spine; lateral carinae II continuous with anteriormost tooth of lateral carina III, surfaces of teeth on lateral carinae somewhat reticulate. Branchiostegal spine not particularly large and extending to less than half of outer margin of laterally extended scaphocerite. Scaphocerite 1.41-1.75 times as long as broad; distolateral tooth smaller than antennal spine and just reaching to far exceeding distal margin of lamella. Pterygostomian spine moderately smaller than antennal spine. Abdomen sculpturing distinct and mainly composed of squamae and nodules but pair of lateral oblique ridges present on each of tergites II to IV. Posterior margins of abdominal tergites II and III deeply notched medially. Abdominal somite II lacking dorsal spine but somite VI usually bearing two pairs of dorsolateral spines. Abdominal pleura always triangular in somite I but broadly triangular or truncate (mostly in males) in other somites, with ventral margins generally not sharp. Posterior margin of abdominal pleuron V only having distal spine and lateral surface of abdominal somite VI bearing oblique anteroventral ridge. Telson generally armed with one pair of small dorsolateral spines. Eggs subspherical and numerous, about 0.4 mm in diameter.

COLORATION. - Not known.

SIZE. - Largest male cl 7.8 mm and largest female cl 12.0 mm. Smallest ovigerous female cl 8.6 mm.

DISTRIBUTION. — Mediterranean, west coast of Africa, the Red Sea and the Indian Ocean to Sri Lanka. At depths of 16-302 m (DE MAN, 1920) but mostly less than 90 m.

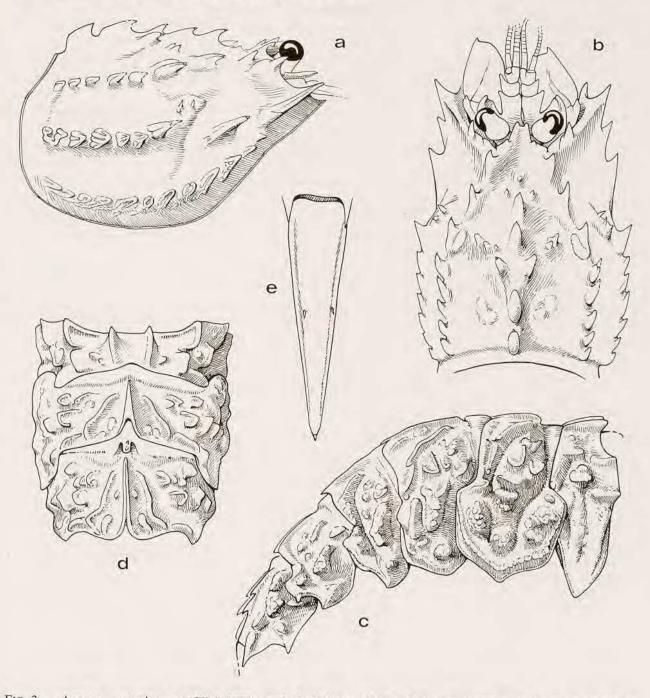


FIG. 2. — Aegaeon cataphractus (Olivi, 1792) : a-d, ♀ 10.9 mm, Gulf of Cadiz, "Talisman", stn 5, 60 m (MNHN-Na 4309) : a, lateral view of carapace; b, dorsal view of carapace and anterior appendages; c, lateral view of abdomen; d, dorsal view of abdominal tergites I-III. — e, ♀ 8.7 mm, Cameroon, "Ombango", st. CH 51, 64 m (MNHN-Na 7783) : dorsal view of telson.

REMARKS. — A. cataphractus is unique in the genus by having many intermediate tubercles on the carapace between the dorsal carina and the lateral carinae I, and the posterior margins of the abdominal tergites II and III deeply notched. Except for a tendency to have slightly fewer intermediate tubercles on the carapace, the material from Madagascar and the Red Sea is almost identical with that from the Mediterranean and the East Atlantic. A similar situation was reported for the material from South Africa (BARNARD, 1950) and India (KEMP, 1916). Moreover, the intermediate tubercles (including those at the hepatic groove) are somewhat more pronounced in the Atlantic specimens.

Amongst the species of *Aegaeon*, the present species is the most similar to *Pontocaris*. Besides having a more robust body and a strong hepatic groove, the abdominal sternites of this species always bear strong median spines even in ovigerous females. Nevertheless, although the thoracic sternites may sometimes touch or even slightly overlap (mostly in small males) the ventral border of the carapace, no well-defined interlocking structure is developed in *A. cataphractus*.

A pair of small and sometimes indistinct dorsolateral spines is usually present at the posterior fourth of the telson in the present species. However, in two specimens one more pair of hardly distinguishable dorsolateral spines is also found near the subdistal end of the telson (ie. altogether two pairs of dorsolateral spines present). Furthermore, some rudimentary projections are observed at the posterior end of the telson in a few specimens. Such variations in the spination of the telson further indicates the intermediate status of the present species between *Aegaeon* and *Pontocaris*. On the other hand, an aberrant specimen with five instead of four dorsal teeth on the carapace was found amongst the material examined in the present study.

Although A. cataphractus is rather common in the shallow waters of the East Atlantic and the Indian Ocean, it has not been collected in the West Pacific despite many intensive surveys in this area. The most eastern distribution of this species is probably limited to Sri Lanka. As pointed out by CALMAN (1939) and RICHARDSON and YALDWYN (1958), the records of this species from New Zealand (e.g. BORRADAILE, 1916) were actually of A. lacazei.

#### Aegaeon lacazei (Gourret, 1887)

Fig. 3

Crangon Lacazei Gourret, 1887 : 1033; 1888 : 35, 143, pl. 12 figs 19-23, pl. 13 fig. 1-10 (type-locality : Gulf of Marseille, France).

Pontocaris habereri Doflein, 1902 : 620, fig. A, pl.1 figs 3-4 (type-locality : Japan). — MIYAKE et al., 1962 : 124. — FUJINO & MIYAKE, 1970 : 298, fig. 22. — TORIYAMA & HAYASHI, 1982 : 104.

Egeon habereri - RATHBUN, 1906 : 911.

Aegeon Brendani Kemp, 1906 : 299 (type-locality : south-west of Ireland).

Aegeon Lacazei - KEMP, 1910a : 156, pl. 22 figs 1-5; 1910b : 413. — DE MAN, 1920 : 293. — CALMAN, 1925 : 17; 1939 : 222. — BALSS, 1927 : 376. — ZARIQUIEY CENARRO, 1935 : 97.

- Aegeon (Pontocaris) Habereri BALSS, 1914a : 71.
- Aegeon cataphractus BORRADAILE, 1916 : 90. Non Olivi, 1792.

Aegeon Habereri - DE MAN, 1920: 293.

Aegeon habereri - YOKOYA, 1933: 43.

Aegeon lacazei - ZARIQUIEY ALVAREZ, 1946 : 90, fig. 116. — BARNARD, 1950 : 814. — DIEUZEIDE, 1950 : 45, fig. 3B. — DIEUZEIDE & ROLAND, 1958 : 60.

Pontocaris lacazei - HOLTHUIS, 1947: 320; 1951: 164; 1952: 59; 1955: fig. 99b; 1980: 152; 1987: 220, unnumbered figs. — ZARIQUIEY ALVAREZ, 1952: 17; 1956: 407; 1962: 33; 1968: 188, figs 78c, 80a-d. — RICHARDSON & YALDWYN, 1958: 40, fig. 44. — MAURIN, 1960: 154; 1961: 531; 1962: 213; 1968: 118. — AUDOUIN, 1965: 174. — ALLEN, 1967: 82. — YALDWYN, 1967; 4. — KUNJU, 1967: 1385. — CROSNIER & FOREST, 1968: 1144; 1973: 250, fig. 81. — KENSLEY, 1969: 155; 1972: 64, fig. 30u; 1981: 28. — LAGARDÈRE, 1970: 1044. — DOMENECH et al., 1981: 155. — MIYAKE, 1982: 68, pl. 23 fig. 5. — CHACE, 1984: 42. — DONG et al., 1986: 5. — KENSLEY et al., 1987: 327. — BRUCE, 1988, fig. 7F (legend erroneously referred to fig. 7E).

Aegaeon lacazei - HOLTHUIS, 1993, fig. 282.

MATERIAL EXAMINED. — Mediterranean Sea. Sicily, Italy: Gulf of Castellamore, 38°6.12'-38°7.06'N, 12°15.48'-12°55.36'E, 350-480 m, 16.6.1974 : 2 spec. (USNM). — Egadi Is. N.W. of Levauzo Is., 38°5.36'-38°8.54'N, 12°12.24-12°19.42'E, 260-360 m, 17.6.1974 : 2 spec. (USNM).

**North East Atlantic**. "*Travailleur*" : stn 1,44°4'N, 5°31'W, 614 m, 6.7.1882 : 1 & 5.2 mm; 2  $\Im$  5.6 and 6.7 mm (MNHN-Na 4315). — Stn 2, 44°5'N, 5°36'W, 608 m, 6.7.1882 : 1 & 7.0 mm; 5  $\Im$  6.3-6.9 mm (MNHN-Na 4313). — Stn 14, 43°24'N, 9°21'W, 400 m, 17.7.1882 : 1 ovig.  $\Im$  7.5 mm (MNHN-Na 4312). — Stn 26, 38°3'N, 9°12'W, 370 m, 24.7.1882 : 1 & 6.2 mm; 1  $\Im$  7.9 mm (MNHN-Na 4311). — Stn 25, 38°6'N, 9°11'W, 460 m, 24.7.1882 : 13 & 5.8-6.3 mm; 9  $\Im$  5.5-8.7 mm (MNHN-Na 4310). — Stn 32, 36°36'N, 7°26'W, 440 m, 25.7.1882 : 1  $\Im$  6.6 mm (MNHN-Na 4314, with a label *Egeon Parfaiti* sp. nov.).

"Thalassa" : st<br/>n W352, 43°38.4'N, 1°55.8'W, 180-270 m, 4.10.1970 : 1 & 7.7 mm; 1 <br/> $\bigcirc$  6.9 mm (MNHN-Na 4300). — St<br/>n W406, 43°55.5'N, 5°44.0'W, 400-700 m, 10.10.1970 : 1 <br/> $\bigcirc$  9.6 mm (MNHN-Na 4301). — St<br/>n W413, 43°50.0'N, 6°08.9'W, 500-540 m, 11.10.1970 : 1 <br/> $\circlearrowright$  7.8 mm (MNHN-Na 4302). — St<br/>n W415, 43°55.1'N, 6°11.3'W, 860-1150 m, 11.10.1970 : 1 <br/> $\circlearrowright$  7.2 mm (MNHN-Na 4303). — St<br/>n W416, 43°50.5'N, 6°11.3'W, 392-850 m, 11.10.1970 : 1 <br/> $\circlearrowright$  7.6 mm; 6 <br/> $\heartsuit$  8.2-9.6 mm (MNHN-Na 4304). — St<br/>n W418, 43°48.3'N, 6°11.0'W, 335-850 m, 11.10.1970 : 3 <br/> $\heartsuit$  9.4-11.4 mm (MNHN-Na 4305).

**Morocco**, **Mauritania**, **Cape Verde Islands**. "*Talisman*" : stn 72, 25°41'N, 15°56'W, 410 m, 1883 : 1 ♀ 9.3 mm (MNHN-Na 1175). — Stn 95, 21°47'N, 17°27'W, 140-155 m, 13.7.1883 : 1 ♂ 7.2 mm; 1 ♀ 8.0 mm (MNHN-Na 1174). — Stn 117, 16°53'N, 25°06'W, 590 m, 29.7.1883 : 1 ♂ 5.7 mm; 10 ♀ 6.2-8.5 mm (MNHN-Na 1173).

**Congo.** Au large de Pointe-Noire. "Ombango" : trawl, 200-250 m, 4.5.1960 : 1 ovig.  $\mathcal{Q}$  8.3 mm (MNHN-Na 7779). — Radiale de Pointe-noire, 300 m, 12.1.1964 : 1  $\mathcal{Q}$  6.6 mm (MNHN-Na 7775). — 5°S, 11°22'E, 190-210 m, sandy mud, 16.3.1967 : 1 damaged  $\mathcal{S}$  (MNHN-Na 7778). — 6°19'S, 11°34'E, 295-305 m, sandy mud, 6.7.1967 : 2 ovig.  $\mathcal{Q}$  9.7-10.2 mm (MNHN-Na 7774). — 255 m, mud, 2.4.1968 : 1 ovig.  $\mathcal{Q}$  10.8 mm (MNHN-Na 7781). — 5°1'S, 11°22'E, 250 m, mud, 16.2.1968 : 1  $\mathcal{Q}$  9.6 mm (MNHN-Na 7782). — 5°9'S, 11°29'E, 245-250 m, mud, 28.2.1968 : 1  $\mathcal{Q}$  10.3 mm (MNHN-Na 7780).

Angola. "Ombango": 11°54'S, 13°28'E, 248-250 m, mud, 17.4.1968 : 1 2 8.9 mm (MNHN-Na 7776).

**Madagascar**. "Vauban" : stn 31, 12°34'S, 48°15'E, 395 m, 13.9.1972 : 1 \overline 7.5 mm (MNHN). — Stn 44, 15°25.7'S, 46°1'E, 200-210 m, 7.11.1972 : 1 \overline 7.9 mm (MNHN).

**Taiwan**. Ta-Chi, I-Lan County, north-eastern Taiwan, fish market, commercial trawlers : 9.9.1984, 2  $\Im$  8.6-9.9 mm (MNHN, NTOU in exchange); 14.10.1984, 1  $\Im$  7.5 mm (NTOU); 29.11.1984, 1  $\Im$  9.6 mm (MNHN, NTOU in exchange); 31.12.1984, 1  $\Im$  8.6 mm (MNHN, NTOU in exchange); 14.5.1988, 1  $\Im$  7.1 mm (MNHN, NTOU in exchange); 1.9.1989, 1  $\Im$  10.0 mm (NTOU); 12.1990, 1  $\Im$  10.2 mm (MNHN, NTOU in exchange); 29.4.1991, 1  $\Im$  7.8 mm (MNHN, NTOU in exchange); 9.1991, 1  $\Im$  6.8 mm (MNHN, NTOU in exchange); 15.4.1993, 1  $\Im$  6.5 mm (NTOU); 27.5.1994, 1  $\Im$  10.0 mm (NTOU).

Su-Aou, I-Lan County, north-eastern Taiwan, fish market, commercial trawlers : 22.5.1990, 2 & 7.6-7.7 mm (MNHN, NTOU in exchange).

Philippines. "Albatross" : stn 5412, 10°09'15"N, 123°52'E, 296 m, 23.3.1909 : 1 & 6.3 mm (USNM).

MUSORSTOM 1 : stn CP 19, 13°57.8'N, 120°18.2'E, 167-187 m, 21.3.1976 : 1 ovig. ♀ 6.3 mm (MNHN-Na 5984). — Stn CP 40, 13°57.4'N, 120°27.8'E, 265-287 m, 24.3.1976 : 1 ♀ 10.8 mm (MNHN-Na 5985). — Stn CP 42, 13°54.1'N, 120°28.6'E, 379-407 m, 24.3.1976 : 1 ♀ 10.1 mm (MNHN-Na 5987).

MUSORSTOM 2 : stn CP 67, 14°0.1′N, 120°18.5′E, 193-199 m, 29.11.1980 : 2 ♀ 9.0-9.3 mm (MNHN-Na 5983). — Stn CP 83, 13°55.2′N, 120°30.5′E, 318-320 m, 2.12.1980 : 2 ovig. ♀ 9.8-11.6 mm (MNHN-Na 5986).

MUSORSTOM 3 : Stn CP 100, 14°N, 120°18′E, 189-199 m, 1.6.1985 : 1 ♂ 7.2 mm; 1 ♀ 9.4 mm (NTOU, MNHN in exchange). — Stn CP 138, 11°54′N, 122°15′E, 252-370 m, 6.6.1985 : 1 ♀ 10.9 mm (MNHN). — Stn CP 143, 11°29′N, 124°11′E, 205-214 m, 7.6.1985 : 1 ♀ 11.8 mm (MNHN).

Indonesia. KARUBAR. *Kai Islands*: stn CP 25, 5°30'S, 132°52'E, 336-346 m, 26.10.1991 : 1 ♀ 8.5 mm (MNHN). — *Tanimbar Islands* : stn DW 49, 8°S, 132°59'E, 206-210 m, 29.10.1991 : 1 ♀ 5.3 mm (MNHN). — Stn CP 67, 8°58'S, 132°6'E, 146-233 m, 1.11.1991 : 3 ♀ 9.3-9.9 mm (MNHN). — Stn CP 79, 9°16'S, 131°22'E, 239-250 m, 3.11.1991 : 1 ♂ 10.5 mm; 1 ♀ 9.3 mm (MNHN). — Stn CP 86, 9°26'S, 131°13'E, 223-225 m, 4.11.1991 : 2 ♀ 9.6-9.7 mm (MNHN).

New Caledonia. "Vauban": 22°17.5'S, 167°12.5'E, 390 m, 23.5.1978: 1 & 6.1 mm (MNHN).

SMIB 6 : stn 137, Grand Passage, 19°0.3'S, 163°18.3'E, 305-330 m, 3.3.1990 : 1 9 7.5 mm (MNHN).

DIAGNOSIS. — Body slender and integument rather soft. Rostrum strongly bifurcate. Carapace about 1.35 (1.28-1.59) times as long as broad; armed with four dorsal teeth; lateral carina I having 7-9 (mostly 8) teeth, with anteriormost tooth minute and distinctly separated from other teeth; no tubercles present between dorsal and lateral carinae I; lateral carina II interrupted by hepatic groove, with anterior part bearing one tooth while posterior part has 5-8 teeth and an additional small tooth on hepatic groove at about lower 1/4 between lateral carinae I and II; lateral carina III provided with 12-16 (mostly 13-16) teeth behind branchiostegal spine; lateral carina II continuous with anteriormost tooth of lateral carina III. Branchiostegal spine not particularly large, usually extending to less than 1/2 (mostly about 1/3) of outer margin of laterally extended scaphocerite. Scaphocerite 1.84-2.22 times as long as broad; distolateral tooth as large as or smaller than antennal spine and usually far exceeding distal margin

of lamella. Pterygostomian spine distinctly smaller than antennal spine. Abdominal sculpturing complicated and consisting of irregularly arranged squamae and interrupted carinae, with only one pair of continuous oblique lateral ridges present on tergites III and IV. Posterior margins of abdominal tergites II and III only moderately notched. Anterior end of dorsal carina on abdominal tergite II produced as a large, hooked spine, while abdominal somite VI generally bears two pairs of dorsolateral spines. Abdominal pleura ranging from triangular and truncate in males to broadly triangular (but with ventral margins pointed) in ovigerous females. Abdominal pleuron V bearing

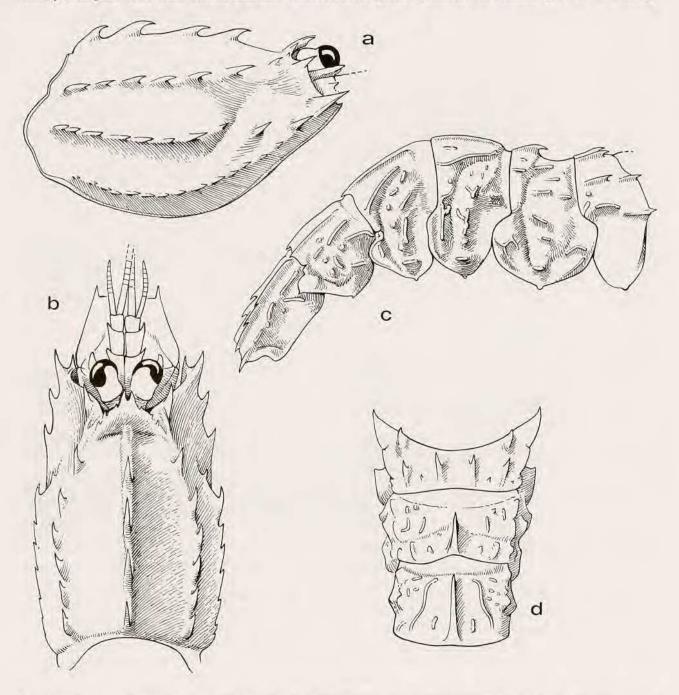


FIG. 3. — Aegaeon lacazei (Gourret, 1887): a-d, Q 9.6 mm, North East Atlantic, "Thalassa", stn W416 (MNHN-Na 4304): a, lateral view of carapace; b, dorsal view of carapace and anterior appendages; c, lateral view of abdomen; d, dorsal view of abdominal tergites I-III.

posterodistal spine only. Lateral surface of abdominal somite VI with oblique anteroventral ridge. Telson with two pairs of dorsolateral and three pairs (outer pair very short, but robust) of terminal spines. Eggs subspherical and numerous, about 0.35 mm in diameter.

COLORATION. — Body varying from yellow to brown, carapace with broad transverse pale or white (in brown specimens) subanterior band. Eyes dark brown. Pereiopod I with distal end of palm whitish. Pleopods pale yellow. Tail fan with subanterior part whitish, posterior part with a broad, red-brown, transverse band.

SIZE. - Largest male cl 10.46 mm and largest female cl 11.8 mm. Smallest ovigerous female cl 6.3 mm.

DISTRIBUTION. — World-wide except western Atlantic. Recorded from the Mediterranean, S.W. Ireland, western Africa, South Africa, Madagascar, Zanzibar, India, Japan, East China Sea, Taiwan, the Philippines, Indonesia, Australia, New Caledonia, New Zealand and Hawaii. At depths of 140-614 m (30-759 m in CROSNIER & FOREST, 1973).

REMARKS. — The different populations in this widely distributed species show some variations. For example, the second anterior dorsal tooth on the carapace is frequently smaller than the anteriormost tooth in the material from Congo (see CROSNIER & FOREST, 1973, fig. 81), while the former is generally as large as, or larger than, the latter in the Philippine specimens. On the other hand, a Hawaiian specimen reported by RATHBUN (1906), as well as one Taiwanese specimen, has five dorsal teeth on the carapace. Furthermore, the spines and carinae on the body of the Philippine material are usually more distinct than those of the specimens from Taiwan. Nevertheless, since these variations, including the shape of the scaphocerite and abdominal sculpturing mentioned by FUJINO and MIYAKE (1970), can often be found within the same population (though they may differ in frequency), it is unwarranted to separate the material from the various localities into different taxa. Thus, we follow CHACE (1984) in synonymizing DOFLEIN'S (1902) species, *A. habereri* from Japan, with *A. lacazei*.

#### Aegaeon rathbuni de Man, 1918

Fig. 4

Egeon orientalis - RATHBUN, 1906 : 911, pl. 23 fig. 3. Non Henderson, 1893.

Aegeon Rathbuni de Man, 1918 : 304 (type-locality : Borneo, Indonesia); 1920 : 300, pl. 24 fig. 74b, pl. 25 figs 74-74a. — CALMAN, 1939 : 221.

Pontocaris rathbuni - CHACE, 1984 : 44.

Pontocaris rathbunae - KENSLEY et al., 1987: 327.

Not Pontocaris rathbuni - HAYASHI, 1986 : 147, fig. 97. [= ? sp.].

MATERIAL EXAMINED. — Indonesia. "Siboga" : stn 89, Pulu Kaniungan Ketjil, Borneo, 1°9'N, 118°53'E, 11 m, 21.6. 1899 : 1 & 6.8 mm (lectotype) (ZMA).

"Albatross" : stn 5661, 5°49'40"S, 120°24'30"E, 329 m, 20.12.1909 : 1 & 7.2 mm (USNM).

KARUBAR. Kai Islands : stn CP 5, 5°49'S, 132°18'E, 296-299 m, 22.10.1991 : 1 & 7.7 mm (MNHN). — Stn CP 12, 5°15'S, 133°1'E, 439-459 m, 24.10.1991 : 1 ovig. & 9.5 mm; 6 & 5.4-10.0 mm (MNHN). — Stn CP 16, 5°17'S, 132°50'E, 315-349 m, 24.10.1991 : 1 & 7.4 mm; 1 & 9.4 mm (NTOU, MNHN in exchange). — Stn CP 20, 5°15'S, 132°59'E, 760-809 m, 15.10.1991 : 3 & 7.5-7.8 mm (MNHN). — Stn CP 35, 6°8'S, 132°45'E, 390-502 m, 27.10.1991 : 1 ovig. & 8.8 mm (MNHN).

**New Caledonia.** MUSORSTOM 4 : stn DW 162, 18°35'S, 163°10.3'E, 525 m, 16.9.1985 : 1  $\Im$  4.7 mm (MNHN). — Stn CP 169, 18°54.3'S, 163°11.2'E, 590 m, 17.9.1985 : 1  $\Im$  5.1 mm; 1  $\Im$  8.4 mm (MNHN). — Stn CP 180, 18°56.8'S, 163°17.7'E, 440 m, 18.9.1985 : 4 ovig.  $\Im$  6.1 -9.1 mm; 5  $\Im$  5.2-8.8 mm (MNHN). — Stn CP 199, 18°50'S, 163°14.5'E, 600 m, 20.9.1985 : 1  $\Im$  8.6 mm (MNHN). — Stn CP 236, 22°11.3'S, 167°15'E, 495-550 m, 2.10.1985 : 1  $\Im$  5.86mm (MNHN). — Stn CP 238, 22°13'S, 167°14'E, 500-510 m, 2.10.1985 : 1  $\Im$  5.1 mm (MNHN).

MUSORSTOM 5 : stn DW 305, 22°9.27'S, 159°24.42'E, 430-440 m, 12.10.1986 : 2 & 4.5-4.6 mm (MNHN).

BIOGEOCAL : stn DW 307, 20°35.38'S, 166°55.25'E, 470-480 m, 1.5.1987 : 1 & 5.6 mm; 1 & 5.2 mm (MNHN).

BIOCAL : stn DW 33, 23°10'S, 167°10'E, 675-680 m, 29.8.1985 : 1 & 5.7 mm (MNHN). — Stn DW 44, 22°47'S, 167°14'E, 440-450 m, 30.8.1985 : 1 & 5.7 mm (MNHN). — Stn CP 45, 22°47'S, 167°15'E, 430-465 m : 1 & 6.2 mm (MNHN). — Stn DW 46, 22°53'S, 167°17'E, 570-610 m, 30.8.1985 : 1 & 5.5 mm (MNHN). — Stn CP 52, 23°6'S,

167°47'E, 540-600 m, 31.8.1985 : 3 ♂ 4.7-6.5 mm (MNHN). — Stn CP 78, 22°16'S, 167°15'E, 445-450 m, 5.9.1985 : 1 ovig. ♀ 8.0 mm (MNHN). — Stn CP 290, 20°36.91'S, 167°3.34'E, 760-920 m, 27.4.1987 : 1 ♀ 6.7 mm (MNHN).

CHALCAL 2 : stn CC 1, 24°54.96'S, 168°21.9'E, 500 m, 28.10.1986 : 1  $\Im$  7.5 mm (MNHN). — Stn CC 2, 24°55.48'S, 168°21.29'E, 500 m, 28.10.1986 : 1  $\Im$  8.9 mm (MNHN). — Stn CP 21, 24°54'S, 168°21.61'E, 510 m, 28.10.1986 : 1  $\Im$  7.5 mm; 2  $\Im$  7.4 and 7.6 mm (MNHN). — Stn DW 74, 24°40.36'S, 168°38.38'E, 650 m, 29.10.1986 : 1  $\Im$  8.0 mm (MNHN). — Stn DW 75, 24°39.31'S, 168°39.67'E, 600 m, 29.10.1986 : 1  $\Im$  7.9 mm (MNHN).

SMIB 3 : stn DW 1, 24°56'S, 168°22'E, 520 m, 20.5.1987 : 1 ♀ 7.1 mm (MNHN). — Stn DW 5, 24°55'S, 168°22'E, 502-512 m, 21.5.1987 : 1 ovig. ♀ 7.5 mm (MNHN).

LAGON : stn CP 1062, 20°14.9'S, 163°53'E, 300-320 m, 5.5.1988 : 1 & 4.7 mm (MNHN).

Loyalty Islands. MUSORSTOM 6 : stn CP 464, 21°2.3'S, 167°31.6'E, 430 m, 21.2.1989 : 1 2 6.3 mm (MNHN).

**Taiwan**. Ta-Chi, I-Lan County, north-eastern Taiwan, fish market, commercial trawlers, about 300 m, 23.5.1990 :  $3 \ 9 \ 9.1-10.8 \ mm \ (NTOU)$ . — No date,  $1 \ 9 \ 9.2 \ mm \ (MNHN, NTOU \ in exchange)$ .

**Hawaii**. "Albatross" : stn 4021, Vic. Kauai Is., 523-730 m : 2  $\Im$  about 6 mm (paralectotypes) (USNM). — Stn 4166, Vic. Modu Mann Is., 537-1464 m : 1  $\Im$  7 mm (paralectotype) (USNM).

**Madagascar**. "Vauban" : stn 1, 12°52'S, 48°10.3'E, 420-428 m, 4.3.1971 : 1 ovig.  $\Im$  8.5 mm; 1  $\Im$  9.3 mm (MNHN). — Stn 2, 12°53.3'S, 48°9.4'E, 480-520 m, 4.3.1971 : 2  $\Im$  8.0 and 8.7 mm (MNHN). — Stn 3, 12°52.3'S, 48°10.4'E, 403-415 m, 4.3.1971 : 1  $\Im$  7.5 mm (MNHN). — Stn 6, 12°42.7'S, 48°12.8'E, 435-444 m, 5.3.1971 : 1  $\Im$  6.3 mm (MNHN). — Stn 9, 12°42'S, 48°13.5'E, 455-460 m, 14.4.1971 : 1  $\Im$  6.1 mm (MNHN). — Stn 39, 12°46.5'S, 48°10.4'E, 495-500 m, 15.9.1972 : 1  $\Im$  7.6 mm (MNHN). — Stn 59, 23°36'S, 43°29.6'E, 600-610 m, 27.3.1973 : 1  $\Im$  8.3 mm (MNHN). — Stn 119, 12°50.7'S, 48°6'E, 750-765 m, 10.10.1974 : 1  $\Im$  8.5 mm (MNHN). — Stn 122, 12°43'S, 41°12'E, 500 m, 11.10.1974 : 1  $\Im$  6.1 mm (MNHN).

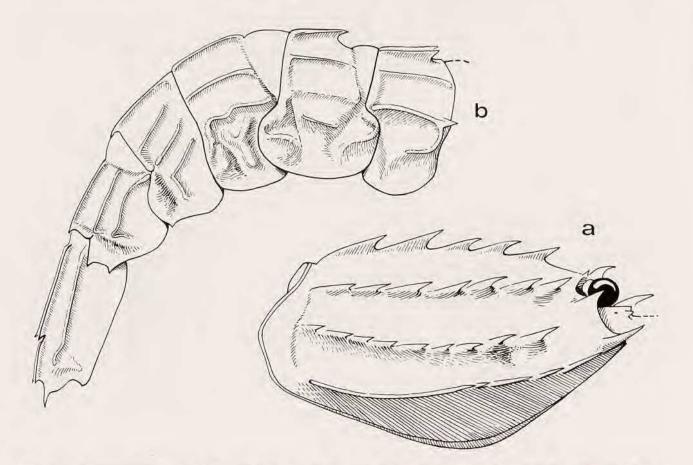


FIG. 4. — Aegaeon rathbuni de Man, 1918 : a-b, \$\varphi\$ 8.0 mm, New Caledonia, CHALCAL 2, stn DW 74, 650 m (MNHN) : a, lateral view of carapace; b, lateral view of abdomen.

DIAGNOSIS. - Body slender and integument rather soft. Rostrum strongly bifurcate. Carapace about 1.52 (1.38-1.72) times as long as broad; usually armed with five dorsal teeth; lateral carina I bearing 7 teeth, anteriormost tooth only slightly smaller and not separated from other teeth; lateral carina II having 7-11 teeth and continuous with antennal spine, though anteriormost tooth slightly shifted downwards by the presence of rudimentary hepatic groove; lateral carina III continuous with branchiostegal spine, bearing 4-8 teeth. Branchiostegal spine not particularly large and extending to less than 1/3 of outer margin of laterally extended scaphocerite. Scaphocerite 1.61-2.06 times as long as broad, with distolateral tooth more or less as large as antennal spine and overreaching distal margin of lamella. Pterygostomian spine much smaller than antennal spine. Abdominal sculpturing rather simple, mainly consisting of two lateral pairs of almost straight longitudinal carinae, continuous from lateral carapacial carinae I and II to abdominal somite V. Median notch in posterior margin of abdominal tergite II slight, absent in tergite III. Dorsal carina of abdominal tergite II sharply pointed anteriorly, while abdominal somite VI bears one pair of dorsolateral spines. Abdominal pleura broadly triangular in males, broadly quadrangular in females. Posterior margin of abdominal pleuron V with both basal and distal spines (distal one smaller). Lateral surfaces of abdominal somite VI without anteroventral ridge. Telson with two pairs of dorsolateral and three pairs (outer pair very short, but robust) of terminal spines. Eggs subspherical and numerous, about 0.45 mm in diameter.

COLORATION. — Body generally orange-brown to red-brown, with scattered darker spots, particularly at anterior margins of carapace and tail fan. Dactylus of pereiopod I whitish. Eyes brown.

SIZE. - Largest female cl 10.8 mm and largest male cl 7.7 mm. Smallest ovigerous female cl 6.1 mm.

DISTRIBUTION. — Indo-West Pacific from Hawaii to Taiwan, Indonesia, S.W. Australia, New Caledonia, Loyalty Islands, Zanzibar and Madagascar. At depths of 11 m (see remarks below) to at least 809 m (possibly 1464 m from Hawaii), mostly more than 300 m.

REMARKS. — The material from the various localities is generally very similar. As mentioned by CHACE (1984), the size of the third dorsal tooth of the carapace is rather variable in this species. In the material from Hawaii, Taiwan and the New Caledonia, this tooth is usually distinctly smaller than the other dorsal carapacial teeth (particularly in small specimens). In four New Caledonian and one Indonesian KARUBAR specimen this tooth is even missing (i.e. only four dorsal teeth present). However, 9 of the 11 specimens from the Madagascar and 7 of the 16 specimens from Indonesia have the five dorsal teeth subequal (the lectotype has the third tooth slightly smaller, see also DE MAN, 1920). As one of the four Taiwanese specimens and five out of the 40 New Caledonian specimens also have the third dorsal tooth on the carapace not much smaller than the other teeth, it seems likely that the differing size of this tooth is merely a natural variation in the various populations of little taxonomic significance.

As mentioned by many authors (e.g. DE MAN, 1920; CHACE, 1984), the general appearance and abdominal sculpturing of *A. rathbuni* are rather similar to those of the species of *Parapontocaris*. An additional pair of weaker longitudinal carinae, which are joined perpendicularly at the posterior ends with the transverse ridges of the corresponding pleura, is present on the abdominal somite IV (i.e. altogether three pairs of lateral longitudinal carinae are present at this somite).

A. rathbuni probably has the deepest distribution of the genus. Except for the lectotype, all the other 73 specimens examined were collected from depths below 269 m depth. Although DE MAN (1918, 1920) mentioned that it was obtained from 11 m deep, the label accompanying the slightly broken lectotype does not have any depth data. It is not known whether the lectotype actually came from a much greater depth or not. On the other hand, one of the paralectotypes was collected from between 537-1464 m. Nevertheless, it is still not certain whether this species occurs in waters deeper than 1000 m.

Although HAYASHI'S (1986) description of the Japanese material fits the present species well, the photograph provided (HAYASHI, 1986, fig. 97) does not belong to *Aegaeon* or the other two genera of the present study. Thus, *A. rathbuni* is not considered to be known from Japan for the time being.

### Aegaeon orientalis Henderson, 1893

Fig. 5

Aegeon orientalis Henderson, 1893 : 446, pl. 40 figs 16-17 (type-locality : Gulf of Martaban, Burma). — KEMP, 1916 : 378. — DE MAN, 1920 : 293.

Aegeon rugulosum Borradaile, 1915 : 210 (type-locality : Maldives).

Aegeon rugulosus - BORRADAILE, 1917: 411, pl. 59 fig. 12.

Aegeon rugulosa - DE MAN, 1920: 293.

Pontocaris orientalis - JOHNSON, 1961 : 60; 1979 : 47. - CHACE, 1984 : 42.

Not Egeon orientalis - RATHBUN, 1906: 911, pl. 23 fig. 3. (= A. rathbuni de Man, 1918).

MATERIAL EXAMINED. - Birmanie. Gulf of Martaban : 1 9 7.27 mm (type, NHM-88.34).

Maldives. Haddumati Atoll : 1 & 4.5 mm (type of Aegeon rugulosus, UMZC-AR.3.1920).

Vietnam. Bay of Nhatrang, stn D.N.3, 1.1.1960-10.4.1960, A. GALLARDO coll. : 1 9 5.3 mm (RMNH-17042).

Philippines. MUSORSTOM 1 : stn 57, 13°52.7'N, 120°13.2'E, 96-107 m. 26.3.1976 : 1 ovig. ♀ 5.8 mm (MNHN). MUSORSTOM 3 : stn CP 121, 12°8'N, 121°18'E, 73-84 m, 3.6.1985 : 1 ♀ 8.4 mm (MNHN). — Stn CP 142, 11°47'N, 123°2'E, 26-27 m, 6.6.1985 : 1 ♀ 6.9 mm (MNHN).

New Caledonia. LAGON : stn 111, 22°24'S, 166°48'E, 25 m, 22.8.1984 : 1 ♀ 6.1 mm (MNHN). -- Stn 113, 22°23'S, 166°48'E, 32 m, 22.8.1984 : 1 & 4.7 mm; 1 & 6.2mm (MNHN). - Stn 120, 22°28'S, 166°43'E, 46 m, 23.8.1984 : 1 & 4.6 mm; 1 & 6.0 mm (MNHN). - Stn 152, 22°33'S, 166°43'E, 23 m, 24.8.1984 : 1 ovig. & 7.1 mm (MNHN). - St. 169, 22°8'S, 166°8'E, 22 m, 18.9.1984 : 1 & 4.6 mm (MNHN). - Stn 234, 22°32'S, 166°51'E, 56 m, 23.10.1984 : 1 & 4.3 mm; 1 & 4.2 mm (MNHN). - Stn 244, 22°25'S, 167°E, 47 m, 23.10.1984 : 1 & 4.6 mm; 2 & 5.7 and 7.1 mm (NTOU, MNHN in exchange). - Stn 282, 22°25'S, 166°23'E, 12 m, 9.11.1984 : 1 & 4.1 mm; 1 & 4.3 mm (MNHN). — Stn 295, 22°42'S, 166°43'E, 41 m, 26.11.1984 : 1 ovig. 9 7.3 mm (MNHN). — Stn 348, 22°42'S, 166°54′E, 45 m, 29.11.1984 : 1 ♂ 4.5 mm (MNHN). — Stn 391, 22°28′S, 167°13′E, 65 m, 22.1.1985 : 1 ♀ 5.0 mm (MNHN). — Stn 403, 22°35'S, 167°18'E, 45 m, 23.1.1985 : 1 ♂ 4.3 mm; 1 ovig. ♀ 5.2 mm (MNHN). — Stn 438, 18°10'S, 162°51'E, 37 m, 25.2.1985 : 1 & 4.6 mm (MNHN). — Stn 523, 19°11'S, 163°39'E, 47 m, 5.3.1985 : 1 ovig. ♀ 6.0 mm (MNHN). — Stn 541, 19°6'S, 163°3'E, 45 m, 25.2.1985 : 1 ♂ 4.2 mm (MNHN). — Stn 560, 22°43'S, 166°57'E, 48 m, 16.7.1985 : 1 9 4.9 mm (MNHN). - Stn 570, 22°50'S, 167°1'E, 53 m, 7.7.1985 : 1 3 4.3 mm (MNHN). — Stn 622, 22°1.7'S, 166°52.7'E, 67 m, 6.8.1986 : 1 ovig. 9 4.5 mm (MNHN). — Stn 702, 21°26.7'S, 166°8.2'E, 37 m, 10.8.1986 : 1 ovig. 9 5.1 mm (MNHN). — Stn 724, 21°19.7'S, 165°57.8'E, 36-38 m, 12.8.1986 : 1 9 4.8 mm (MNHN). — Stn 816, 21°52.6'S, 165°25.4'E, 31 m, 10.1.1987 : 1 8 4.1 mm (MNHN). — Stn 932, 20°46.3'S, 164°16.5'E, 23 m, 27.4.1988 ; 1 ovig. \$ 5.2 mm (MNHN). - Stn 948, 20°32.2'S, 164°8.8'E, 16 m, 28.4.1988 : 1 ovig. 9 7.1 mm (MNHN). - Stn 1073, 19°59.8'S, 164°3'E, 28 m, 23.10.1989 : 2 9 6.8 and 7.6 mm (MNHN). - Stn 1128, 19°31.2'S, 163°52.2'E, 26 m, 26.10.1989 : 4 9 4.5-5.5 mm (MNHN). - Stn 1129, 19°29.2'S, 163°48.8'E, 40 m, 26.10.1989 : 2 & 4.1 and 4.3 mm; 1 ovig. 9 5.4 mm; 1 9 5.5 mm (MNHN). - Stn 1138, 19°26.5'S 163°46.5'E, 42 m, 26.10.1989: 1 ovig. 9 5.1 mm (MNHN). — Stn 1174, 19°21.2'S, 163°13.7'E, 53 m, 31.10.1989 : 1 & 4.2 mm; 1 & 5.2 mm (MNHN). — Stn 1181, 19°23.9'S, 163°14.7'E, 45 m, 31.10.1989 : 1 & 3.9 mm (MNHN). — Stn 1190, 19°34.2'S, 163°30.8'E, 40 m, 1.11,1989: 1 ovig. 9 4.7 mm (MNHN). — Stn 1197, 19°35.6'S, 163°22.1'E, 41 m, 1.11.1989 : 1 § 3.7 mm (MNHN).

Chesterfield Islands. CHALCAL 1 : stn CP 11, 20°4.4'S, 158°47.41'E, 300 m, 22.7.1984 : 1 ♂ 3.4 mm (MNHN). — Stn DC 20, 19°11.6'S, 158°42,1'E, 67 m, 17.7.1984 : 1 ovig. ♀ 5.2 mm (MNHN). — Stn DC 53, 21°19.5'S, 158°55.3'E, 60 m, 24.7.1984 : 1 ♂ 5.5 mm (MNHN).

CORAIL 2 : stn DW 62, 19°14.99'S, 158°50.98'E, 64 m, 24.8.1988 : 1  $\stackrel{\circ}{\sigma}$  4.1 mm (MNHN). — Stn DW 128, 19°27.89'S, 158°30.44'E, 38 m, 29.8.1988 : 3  $\stackrel{\circ}{\circ}$  5.2-7.4 mm (MNHN). — Stn DW 152, 19°52'S, 158°20'E, 51 m, 1.9.1988 : 1  $\stackrel{\circ}{\sigma}$  4.2 mm (MNHN).

**Gulf of Aden**. Off Yemen, "*Meteor*", Cruise 5 : stn 236, beamtrawl, 12°19'N, 43°27.1E, 35-45 m, 6.3.1987 : 12 spec. (SMF). — Stn 283, 12°30.9'N, 44°47.7'E, 76 m, 16.3.1987 : 13 spec. (SMF).

DIAGNOSIS. — Body somewhat stout and integument rather soft. Rostrum weakly tridentate. Carapace about 1.2 (1.07-1.32) times as long as broad; usually armed with five low teeth on dorsal carina; lateral carina I bearing 6-7 teeth, with anteriormost tooth as large as, and not distinctly separated from, other teeth; lateral carina II having 6-8 teeth and with anteriormost tooth situated slightly downwards; lateral carina III continuous with branchiostegal spine and bearing 5-10 teeth. Hepatic groove rudimentary. Branchiostegal spine not particularly large, failing to reach 1/3 of outer margin of laterally extended scaphocerite. Scaphocerite about 1.38 (1.25-1.58) times as long as broad, with distolateral tooth distinctly smaller than antennal spine, but more or less reaching distal margin of lamella. Pterygostomian spine much smaller than antennal spine. Abdominal sculpturing mainly composed of one

pair of curved mesial ridges and another pair of interrupted lateral ridges. Posterior margin of abdominal tergite II deeply notched, but that of tergite III only slightly notched medially. Dorsal carina of abdominal tergite II sharply pointed anteriorly, while somite VI bears one pair of dorsolateral spines. Abdominal pleura from broadly triangular in males to broadly quadrangular in spawning females. Posterior margin of abdominal pleuron V bearing only distal spine, lateral surfaces of abdominal somite VI without anteroventral ridge. Telson with two pairs of dorsolateral and two pairs (dorsally and ventrally, the former short) of terminal spines. Eggs subspherical and numerous, about 0.5 mm in diameter.

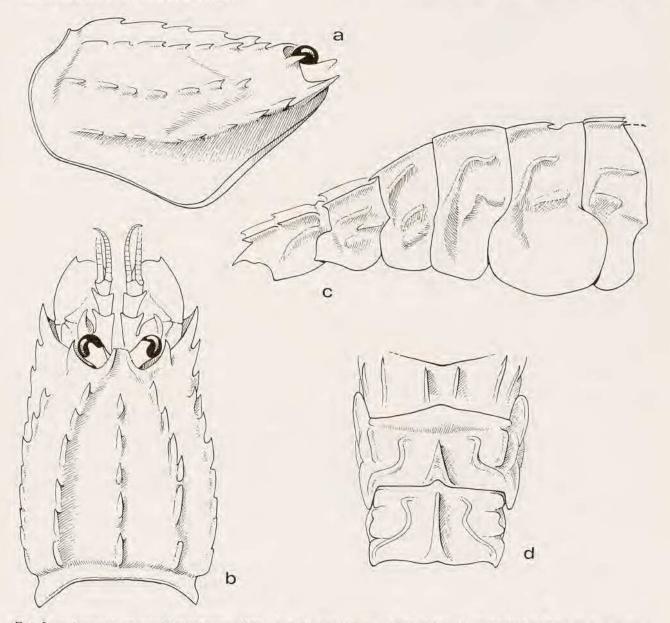


FIG. 5. — Aegaeon orientalis Henderson, 1893 : a-d, ♀ type 7.3 mm, Gulf of Martaban (BMNH-88.34) : a, lateral view of carapace; b, dorsal view of carapace and anterior appendages; c, lateral view of abdomen; d, dorsal view of abdominal tergites I-III.

COLORATION. - Not known.

SIZE. - Largest male cl 5.5 mm and largest female cl 8.4 mm. Smallest ovigerous female cl 4.5 mm.

DISTRIBUTION. — Indo-West Pacific from the Gulf of Aden to the Persian Gulf, Maldives, India, Andaman Sea, Singapore, Vietnam, Philippines, Chesterfield Islands and New Caledonia. At depths of 12-107 m, except one specimen from the Chesterfiel Islands collected at 300 m.

REMARKS. — Thanks to the abundant material from New Caledonia, the characteristics of this previously little known species are now clearer. The type (female) from the Gulf of Martaban is in good condition and very similar to the material from the various localities. *A. rugulosum* described by BORRADAILE (1915) from the nearby Maldives was also very poorly known due to the brief original description. An examination of BORRADAILE's (1915) type (male in good condition, though stated to be damaged by BORRADAILE) reveals that it actually belongs to the species described by HENDERSON (1893). *A. rugulosum*, therefore, should be treated as a junior synonym of *A. orientalis*.

Although having a rather stout body and broad scaphocerite, A. orientalis is essentially closer to Parapontocaris than to Pontocaris. At first glance the rostrum of this species appears to be truncate, but three microscopic teeth are actually present at the apex. Although the central tooth may occasionally be minute and not situated exactly in the middle, the tridentate rostrum of A. orientalis looks very much like a degenerated rostrum of Parapontocaris. Furthermore, the median spines on the abdominal sternites are all reduced to tubercles in the females of this species.

Of the 87 specimens examined, one female has 6 dorsal teeth on the carapace while another specimen bears four dorsal teeth only. Furthermore, the teeth on the body of this species are generally low and in some specimens the dorsal spine on the abdominal somite II may be almost leveled.

#### Aegaeon boschii (Christoffersen, 1988)

Fig. 6

Pontocaris sp. - BOSCHI. 1976 : 63; 1979 : 136. Pontocaris boschii Christoffersen, 1988 : 49, figs 2-3 (type-locality : Buenos Aires, Argentina).

MATERIAL EXAMINED. — Uruguay. "W. Besnard" : stn 1645, 34°11'S, 52°19'W, 61 m, 16.1.1972 : 1 & 6.4 mm; 2 ovig. & 7.2 and 7.4 mm, paratypes (NTOU, ex UFPB 4306 in part, exchange); 1 & 8.4 mm (MNHN 12931, ex UFPB 4306 in part, exchange).

DIAGNOSIS. - Body slender and integument rather soft. Rostrum tridentate. Carapace about 1.37 (1.29-1.41) times as long as broad; usually armed with four dorsal teeth; lateral carina I having 6-7 teeth, with anteriormost tooth small and somewhat separated from other teeth; lateral carina II bearing 6-7 regularly arranged teeth; lateral carina III continuous with branchiostegal spine and having 6-10 teeth. Hepatic groove absent or very rudimentary. Branchiostegal spine not particularly large and extending to 1/4-1/3 of outer margin of laterally extended scaphocerite. Scaphocerite about 1.85 (1.59-2.04) times as long as broad, with distolateral tooth slightly smaller than antennal spine and more or less reaching distal margin of lamella. Pterygostomian spine much smaller than antennal spine. Abdominal sculpturing mainly composed of one pair of curved mesial ridges (only those at tergite I interrupted subanteriorly) and another pair of interrupted lateral ridges. Posterior margin of abdominal tergite III not notched, while that of tergite II slightly notched medially. Dorsal carina of abdominal tergite II sharply pointed anteriorly; somite VI bearing one pair of dorsolateral spines. Abdominal pleura from broadly triangular to broadly quadrangular in ovigerous females. Posterior margin of abdominal pleuron V with well-developed basal spine and distal angle also somewhat pointed. Distinct anteroventral ridge present on lateral surface of abdominal somite VI. Telson bearing two pairs of dorsolateral spines and with posterior end having one pair of short spines and another pair of long stiff setae. Eggs ovoid and numerous, with diameters of about 0.4x0.6 mm.

COLORATION. - Not known.

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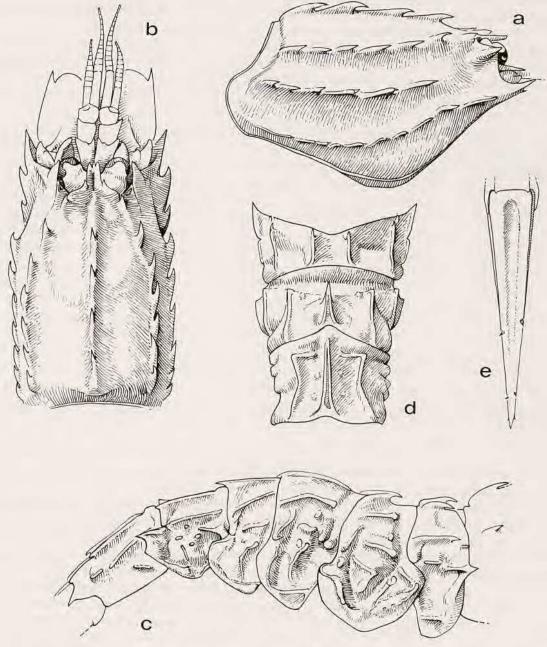


FIG. 6. — Aegaeon boschii (Christoffersen, 1988) : a-e, ♀ paratype 8,4 mm, Uruguay, "W. Besnard", stn 1645, 61 m (MNHN-Na 12931) : a, lateral view of carapace; b, dorsal view of carapace and anterior appendages; c, lateral view of abdomen; d, dorsal view of abdominal tergites I-III; e, dorsal view of telson.

SIZE. — The size of the present species is not mentioned by CHRISTOFFERSEN (1988); the male in the present study is cl 6.4 mm and the three females are cl 7.2 (ovigerous)-8.4 mm.

DISTRIBUTION. — Restricted to the south-western Atlantic from Brazil to Argentina, at depths of 23-169 m (CHRISTOFFERSEN, 1988).

REMARKS. — When describing the present species, CHRISTOFFERSEN (1988) discussed at length its generic relationship with *Parapontocaris* and *Pontocaris* (*sensu* CHACE, 1984), and later believed that it should belong to BRUCE's (1988) *Pontocheras* (CHRISTOFFERSEN, pers. comm.). However, the characters of this western Atlantic species were only very briefly described by CHRISTOFFERSEN (1988). A re-examination of four paratypes of this species shows that their posterior thoracic sternites are not locked with the carapace and the pereiopods are not modified in spawning females. In fact, this species should be placed in *Aegaeon* as defined here for its intermediate characters such as the tridentate rostrum, slender body and the middle of the abdominal sternites armed with strong spines in males.

Although the species occurr in widely separated areas, the tridentate rostrum of *A. boschii* resembles that of *A. orientalis* from the Indo-West Pacific. The abdominal sculpturing is also quite similar, with only the lateral ridges slightly less curved but sharper in *A. boschii*. The more distinct tridentate of the rostrum, the smaller and distinctly separated anteriormost tooth of the lateral carina I and the teeth on the lateral carina II regularly arranged (i.e. no signs of shifting upwards or downwards at the anterior first and second teeth) make the carapace of *A. boschii* most similar to that of *Parapontocaris* amongst the species of *Aegaeon*. With respect to the abdominal sculpturing, however, only the somite III of *A. boschii* is more similar to *Parapontocaris* than in *A. rathbuni*. Thus, amongst the five species currently recognized in *Aegaeon*, it is the carapace of *A. boschii* but the abdomen of *A. rathbuni* that are most similar to those of *Parapontocaris*.

#### Genus PONTOCARIS Bate, 1888

Pontocaris Bate, 1888 : 495 (Gender : feminine, type-species : Pontocaris propensalata Bate, 1888). — ORTMANN. 1895 : 175. — CHACE, 1984 : 41. — CHRISTOFFERSEN, 1990 : 99. — HOLTHUIS, 1993 : 296.

Pontocharis - TORTONESE, 1958: 194.

Pontacris - LAGARDÈRE, 1973 : 126.

Pontocheras Bruce, 1988 : 213 (Gender : masculine, type-species : Pontocheras arafurae Bruce, 1988). — CHRISTOF-FERSEN, 1990 : 99.

DIAGNOSIS. — Body robust and shell hard. Rostrum very short, with tip cleft or entire; only one pair of small, sometimes inconspicuous, lateral teeth present near base. Carapace 1.09-1.43 times as long as broad; dorsal carina with 7-11 teeth; lateral carina I bearing 6-10 teeth, with anteriormost tooth somewhat separated from others; hepatic groove strong and interrupting lateral carina II; lateral carina II on same level with branchiostegal spine, with 1-2 teeth at anterior part and 2-9 teeth or tubercles at posterior part; lateral carina III bearing 0-17, sometimes hardly distinguishable, tubercles and continuous with pterygostomian spine. Branchiostegal spine huge, often expanded and even wing-like, reaching to at least 2/3 of outer margin of laterally extended scaphocerite. Pterygostomian spine from smaller to larger than antennal spine. Scaphocerite broad, 1.09-1.85 times as long as wide, with distolateral tooth smaller than antennal spine and not nearly reaching to slightly overreaching distal margin of lamella. Thoracic sternum with at least posterior three sternites bearing lateral expansions interlocking with ventral border of carapace. Pair of strong ventral teeth present behind coxae of pereiopods V in males and non-spawning females while carpi of pereiopods II distinctly lengthened and/or dactyli of pereiopods V markedly modified in females after spawning molt. Abdominal sculpturing complicated and subdivided, with ridges and lobes irregularly arranged. Abdominal sternites always armed with strong median spines (even in ovigerous females). Abdominal pleura triangular and ventrally pointed in various degree. Telson devoid of spines.

DISTRIBUTION. — Indo-West Pacific including the Red Sea, but mostly concentrated in the Indo-Malay region. At depths of 9-1424 m.

REMARKS. — Although CHACE (1984) only recognized three species in the *P. propensalata* group, the results of the present study show that the names *P. affinis* (Alcock, 1901) and *P. hilarula* (de Man, 1918) should be revived. With the discovery of four more new species and one new subspecies, the members in this group now increase to at least 9 species and one subspecies. On the other hand, BRUCE (1988) found that his new species from

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the Arafura Sea has some peculiar structures such as the posterior thoracic sternites interlocked with the carapace and the dactylus of the last pereiopod remarkably modified. BRUCE (1988) therefore established a new genus Pontocheras to accommodate P. arafurae. However, the "Pontocaris" (sensu CHACE, 1984) material (i.e. A. lacazei and A. cataphractus) used by BRUCE (1988) for comparisons did not belong to the P. propensalata group. It is now found that actually all the species of the P. propensalata group have both of the above characters. Furthermore, the pereiopods are only modified in females at the spawning molt [BRUCE's (1988) specimens were all spawning females], in two ways. In males and non-spawning females, the carpus of the pereiopod II is subequal in length to the chela and the dactylus of the pereiopod V is more or less simple. When females molt for spawning, either the dactylus of pereiopod V becomes variably "subchela" or the carpus of pereiopod II is significantly lengthened. In a new species and subspecies from the Red Sea, P. profundior and P. affinis allodactylus, it is even found that both modifications of the pereiopods II and V occur together in their spawning females. Such polymorphism of the pereiopods of the females was not known previously in the carideans, though both ALCOCK (1901) and DE MAN (1920) had already noticed that the differences in length of pereiopod II in some adult females of P. affinis and P. sibogae are unusual. Furthermore, the shape of the dactylus of pereiopod V in spawning females is often a good taxonomical character for separating the species.

BRUCE (1988) questioned the function of the expanded dactylus of the pereiopod V. It is now known that the shape of the dactylus is related to the sexes and the different developmental stages. The modification of the dactylus of pereiopod V into a "subchela" in the spawning females of these species is analogous to the situation in spiny lobsters (Palinuridae), and is probably also used for the care and/or cleaning of the eggs. Similarly, in those species with the dactylus of pereiopod V not modified, the carpus of pereiopod II is considerably lengthened in spawning females, probably to enable the corresponding chela to reach and clean the eggs.

The interlocking mechanism between the thoracic sternum and the carapace is formed by some pointed lateral expansions on the thoracic sternites VI to VIII (sometimes also V) which clip into certain scalloped fossae developed on the ventral border of the carapace (see BRUCE, 1988, fig. 7B). Moreover, a strong hook is developed on the inner surface of the anterior carapace and securely attached to a small knob on the anterolateral coxa of maxilliped III. A similar hook on the anteromesial carapace is also found in other crangonid species, such as in Vercoia (DURIS, 1992) and in A. cataphractus (present study). In Parapontocaris, A. lacazei and A. rathbuni, only a low, convex lobe is present on the corresponding area of the carapace and is not locked with maxilliped III. In A. orientalis this lobe is somewhat triangular, while it is twisted and forms a rudimentary hook in A. boschii, but still no interlocking with maxilliped III is observed in these two species. On the other hand, none of the above species has the posterior thoracic sternites interlocked with the carapace. Only in Glyphocrangon (two species in the Taiwanese material examined) is a similar and even more secure interlocking mechanism found between the carapace and the thoracic sternites as well as maxilliped III. In view of the hardened and spiny body of these shrimps as well as their behaviour of feigning death (SANKOLLI & SHENOY, 1979), the purpose of such interlocking mechanism is probably for defense by reinforcing the carapace and securing the branchial cavity (i.e. analogous to the cardiac notch in the alpheids; CHACE & KENSLEY, 1992), in addition to the function of preventing the fouling of the branchial chamber, as suggested by BRUCE (1988) and DURIS (1992). Some others relevant behaviours of these shrimps, reared in the laboratory have been reported by SANKOLLI and SHENOY (1979).

The probable stridulating organ at the base of the carpus of pereiopod III, mentioned by BRUCE (1988), is not observed in any of the members of the P. propensalata group, including P. arafurae. Considering the size of these shrimps, such a minute organ, if really present, would be very obscure even under high magnifications. Thus, I have strong reservations about BRUCE's (1988) interpretation that the carpus of pereiopod III bears a stridulating organ in these species. Nevertheless, both the posterior thoracic sternites interlocked with the carapace, as well as the pereiopods distinctly modified in spawning females, are quite enough to separate the P. propensalata group from the other carideans. Therefore, the differences between the members of the P. propensalata group and the other species of "Pontocaris" (sensu CHACE, 1984) are, at least as significant, as those between the latter and Parapontocaris. If the genus Parapontocaris is retained only for those species assigned by CHACE (1984), it then becomes unavoidable to treat the P. propensalata group as a genus of its own and put the rest of the species in

another genus. Since *P. propensalata* was selected by HOLTHUIS (1947) as the type-species of *Pontocaris*, the name *Pontocaris* Bate, 1888, has priority over *Pontocheras* Bruce, 1988, and this genus is now restricted to only the members of the *P. propensalata* group.

With the inclusion of *P. arafurae*, 10 species and one subspecies are now known in *Pontocaris*. Previous workers (e.g. ALCOCK, 1901; DE MAN, 1920; CHACE, 1984) mainly used the number of protuberances in the lateral carapacial carinae and the shape of the abdominal pleura to separate the species of this group. However, there are large variations in these two characters. Furthermore, the shapes of the branchiostegal spine and the ventral margins of the abdominal pleura may vary considerably with sex and age (e.g. the branchiostegal spine is generally shorter and less projecting outwards in males and large specimens). It is also interesting that the branchiostegal spine is often larger and directed more outwards in the more southern populations of the same species. The abundant material in the present study shows that besides the pereiopod modification in spawning females, the shape of the lateral carinae on the abdominal tergites and the median carination on thoracic sternite VI are comparatively constant and useful in distinguishing the species.

#### Key to the species of the genus Pontocaris

1. Lateral sinuous ridges on abdominal tergite II not interrupted <i>P. propensalata</i> — Lateral sinuous ridges on abdominal tergite II interrupted 2
<ul> <li>2. Abdominal somite III armed with an anterodorsal tooth; branchiostegal spine exceptionally long</li></ul>
<ul> <li>3. Abdominal somite IV without distinct posteromedian spine and anterior part of lateral carina II on carapace armed with only 1 tooth</li></ul>
<ul> <li>4. Lateral sinuous ridges on abdominal tergite III not dorsally interrupted</li></ul>
<ul> <li>5. Lateral sinuous ridges on abdominal tergite III usually interrupted near lateral ends; abdominal pleura ventrally truncate or round</li></ul>
<ul> <li>6. Abdominal somite V bearing dorsolateral spine(s); carpus of pereiopod II more than 1.4 times as long as chela in spawning females</li></ul>
7. Pereiopod V simple in spawning females
8. Pterygostomian spine distinctly lower than branchiostegal spine; abdominal pleuron IV without posterodistal tubercle; median tooth of thoracic sternite VI robust and moderately curved; maximum size about cl 21 mm and spawning females larger than cl 15 mm
<ul> <li>Branchiostegal and pterygostomian spines more or less on same level; abdominal pleuron IV usually with at least one side bearing posterodistal tubercle; median tooth of thoracic sternite VI strongly curved but slender; maximum size less than cl 14 mm</li></ul>

## Pontocaris propensalata Bate, 1888

#### Fig. 7

Pontocaris propensalata Bate, 1888 : 496, pl. 86 fig. 5, pl. 90 figs 2-3 (type-locality : Kai Islands, Indonesia). - ORTMANN, 1895 : 175.

Pontocaris media Alcock & Anderson, 1899a : 282 (type-locality : Andaman Sea); 1899b, pl. 41 figs 6-6a. Aegeon medium - ALCOCK, 1901 : 120.

Aegeon propensalata - KEMP, 1916 : 377. - DE MAN, 1920 : 292.

Not Pontocaris propensalata - CHACE, 1984 : 42 [= P. hilarula (de Man, 1918) and P. sibogae (de Man, 1918)].

? Pontocaris propensalata - WHITELEGGE, 1900 : 198.

? Pontocaris pennata - LALITHA DEVI, 1986 : 171, fig. 4. Non Bate, 1888.

MATERIAL EXAMINED. — Indonesia. "Challenger" : stn 192, Kai Islands, 5°49.15'S, 132°14.15'E, 256 m, 26.9.1874 : 1 & 10.7 mm (type, BMNH-88.22).

**Philippines.** MUSORSTOM 1 : stn 16, 13°59'N, 120°10.5'E, 150-164 m, 20.3.1976 : 1 & 8.4 mm; 5  $\Im$  8.1-11.3 mm (MNHN-Na 6005). — Stn 23, 14°N, 120°18.2'E, 189 m, 22.3.1976 : 1 & 7.8 mm (MNHN-Na 6003). — Stn 26, 13°59.5'N, 120°16.8'E, 189 m, 22.3.1976 : 1  $\Im$  11.7 mm (MNHN-Na 6001). — Stn 58, 13°58'N, 120°13.7'E, 143-178 m, 26.3.1976 : 9 & 5.9-9.8 mm; 1  $\Im$  11.0 mm (MNHN-Na 6000). — Stn 62, 13°59.5'N, 120°13.7'E, 179-194 m, 27.3.1976 : 1 & 7.7 mm; 1  $\Im$  11.5 mm (MNHN-Na 6002). — Stn 72, 14°11.8'N, 120°28.7'E, 122-127 m, 28.3.1976 : 1 & 8.5 mm (MNHN-Na 6006).

MUSORSTOM 2 : stn 4, 13°59.4'N, 120°18.4'E, 183-190 m, 20.11.1980 : 1 ♀ 11.9 mm (MNHN-Na 6004). — Stn 6, 13°56.4'N, 120°20.7'E, 136-152 m, 20.11.1980 : 4 ♂ 8.9-9.4 mm; 3 ♀ 7.0-12.1 mm (MNHN-Na 5999).

MUSORSTOM 3 : stn 88, 14°00.5'N, 120°17.4'E, 183-187 m, 31.5.1985 : 2 & 9.8 and 8.3 mm; 6 & 9.2-10.9 mm (MNHN). — Stn 96, 14°00.3'N, 120°17.3'E, 190-194 m, 1.6.1985 : 1 & 8.4 mm (MNHN). — Stn 100, 14°00.0'N, 120°17.6'E, 189-199 m, 1.6.1985 : 2 & 9.5 and 10.7 mm (MNHN). — Stn 103, 14°00.4'N, 120°18.1'E, 193-200 m, 1.6.1985 : 1 & 10.1 mm (MNHN). — Stn 107, 14°01.9'N, 120°27.9'E, 111-115 m, 2.6.1985 : 1 & 12.4 mm (MNHN). — Stn 110, 13°59.5'N, 120°18.2'E, 187-193 m, 2.6.1985 : 1 & 9.1 mm (MNHN). — Stn 111, 14°00.1'N, 120°17.5'E, 193-205 m, 2.6.1985 : 1 & 10.3 mm (MNHN). — Stn 124, 12°02.6'N, 121°35.3'E, 120-123 m, 4.6.1985 : 4 & 7.3-9.7 mm; 3 & 7.3-9.1 mm (MNHN).

**New Caledonia**. LAGON : stn 386, 22°37'S, 167°9'E, 128 m, 22.1.1985 : 1  $\Im$  5.2 mm (MNHN). — Stn 496, 19°04'S, 163°10'E, 200-215 m, 3.3.1985 : 1  $\Im$  10.7 mm (MNHN). — Stn 537, 19°07'S, 163°22'E, 200 m, 6.3.1985 : 1  $\Im$  7.4 mm (MNHN). — Stn 538, 19°07'S, 163°21'E, 195 m, 6.3.1985 : 2  $\Im$  5.3 and 5.8 mm (MNHN). — Stn 539, 19°5'S, 163°17'E, 240 m, 6.3.1985 : 2 juv. 3.9 and 4.0 mm (MNHN).

MUSORSTOM 4 : stn 149, 19°07.6'S, 163°22.7'E, 155 m, 14.9.1985 : 3 postlarvae about 3.5 mm (MNHN). — Stn 151, 19°07'S, 163°22'E, 200 m, 14.9.1985 : 1 & 8.0 mm (MNHN). — Stn 162, 18°35'S, 163°10.3'E, 525 m, 16.9.1985 : 1 & 6.8 mm; 2 & 3.6-4.3 mm (MNHN). — Stn 171, 18°57.8'S, 163°14'E, 425 m, 17.9.1985 : 1 & 11.7 mm (MNHN). — Stn 172, 19°01.2'S, 163°16'E, 275-330 m, 17.9.1985 : 1 & 5.3 mm (MNHN). — Stn 173, 19°02.5'S, 163°18.8'E, 250-290 m, 17.9.1985 : 1 & 8.9 mm (MNHN). — Stn 189, 19°07.5'S, 163°29'E, 210 m, 19.9.1985 : 2 & 7.3 and 9.4 mm (MNHN).

SMIB 6 : stn DW 127, 19°06.8'S, 163°22.6'E, 190-205 m, 4.3.1990 : 1 & 9.0 mm (MNHN).

Loyalty Island. MUSORSTOM 6 : stn CP 419, 20°41.65'S, 167°03.7'E, 283 m, 16.2.1989 : 1 ♀ 5.2 mm (MNHN). — Stn DW 462, 21°05.1'S, 167°26.85'E, 200 m, 21.2.1989 : 2 ♀ 4.1 and 4.5 mm (MNHN). **Chesterfield Island.** CHALCAL 1 : stn CP 10, 20°00.2'S, 158°46.6'E, 225 m, 22.7.1984 : 1 & 8.9 mm (MNHN). MUSORSTOM 5 : Stn 334, 20°06.27'S, 158°47.62'E, 315-320 m, 15.10.1086 : 1  $\bigcirc$  9.2 mm (MNHN). — Stn 335, 20°3.24'S, 158°45.35'E, 315 m, 15.10.1986 : 1  $\bigcirc$  7.3 mm (MNHN). — Stn 346, 19°39.77'S, 158°27.07'E, 245-252 m, 17.10.1986 : 1  $\oslash$  9.5 mm (MNHN). — Stn 376, 19°51.1'S, 158°29.8'E, 280 m, 20.1.1986 : 1  $\heartsuit$  10.2 mm (carapace only and tentatively assigned to the present species, MNHN).

CORAIL 2 : stn CP 131, 19°25.49'S, 158°37.9'E, 215-217 m, 29.8.1988 : 2 & 7.5 and 9.0 mm; 2 ♀ 7.1 and 11.0 mm (MNHN). — Stn CP 162, 19°46.24'S, 158°25.67'E, 203-208 m, 1.9.1988 : 1 & 6.5 mm; 1 ♀ 7.8 mm (MNHN).

DIAGNOSIS. — Tip of rostrum entire (mostly) or microscopically cleft. Carapace about 1.17 (1.1-1.23) times as long as wide; dorsal carina bearing 9-10 teeth; lateral carina I armed with 8-9 teeth; lateral carina II having two teeth on anterior part and 5-7 teeth or tubercles on posterior part; lateral carina III usually with 10-14 tubercles. Scaphocerite about 1.36 (1.22-1.53) times as long as broad. Branchiostegal spine large and wing-like, generally directed moderately outwards in females, but only slightly outwards in males, reaching about 4/5 (2/3-1) in females and 3/4 (2/3-4/5) in males of outer margin of laterally extended scaphocerite. Pterygostomian spine distinctly larger than antennal spine, well below it and generally more or less extending to tip of branchiostegal spine. Pereiopod II with carpus subequal (1.03-1.09 times) in length to chela, even in spawning females. Dactylus of pereiopod V distinctly modified in spawning females; dactylus bifurcate and with outer spine flanked by long flap and setae. Thoracic sternite VI always armed with large, hooked, median tooth. Abdominal sculpturing distinct and subdivided, lateral sinuous ridges of both abdominal tergites II and III continuous. Abdominal somite IV bearing strong posteromedian spine. Abdominal somite V usually lacking dorsal spine but somite VI generally bearing two pairs (range 3-5) of dorsolateral spines. Abdominal pleura with ventral margins truncate in males, less so and somewhat round to bluntly angular in females. Posterodistal tubercles generally present on abdominal pleuron IV, but absent on pleuron V.

COLORATION. — Body pale pink dorsally and pink ventrally. Eyes light brown. Broad transverse pale bands covering mid-carapace and tail-fan. Branchiostegal spine pink. Antennal flagella somewhat banded with brown and white.

SIZE. - Largest female cl 12.4 mm and largest male cl 10.7 mm. Smallest spawning female cl 11.3 mm.

DISTRIBUTION. — Only known with certainty from the Andaman Sea, Philippines, Indonesia, New Caledonia, Chesterfield and Loyalty Islands. At depths of 100-525 m.

REMARKS. — The "Challenger" type from the Kai Islands is still in very good condition, except that the left part of the carapace was removed for illustration of the gills (BATE, 1888, pl. 86 fig. 5). The material from the Philippines and New Caledonia (including adjacent areas) are generally very similar to the type, except that the branchiostegal spine tends to be directed more outwards (sometimes rather strongly) in the New Caledonian specimens. Furthermore, the anteriormost teeth of both the anterior and posterior parts of the lateral carapacial carina II are more protruded and very pronounced (even compared to the other species) in the New Caledonian material.

The ventral margins of the abdominal pleura in the type (male) are remarkably truncate and many authors (e.g. ALCOCK, 1901; DE MAN, 1920; CHACE, 1984) used this as an important character to separate *P. propensalata* from the other species of the genus. However, quite often the ventral margins of the abdominal pleura in the present species are not so truncate, with those of the anterior pleura even being round or bluntly angular (mostly in females and small specimens). Nevertheless, *P. propensalata* can be readily distinguished from the other species of the genus by the lateral sinuous ridges on abdominal tergite II not interrupted.

Pontocaris media, described by ALCOCK and ANDERSON (1899a) from the Andaman Sea, is generally treated as a junior synonym of the present species (e.g. KEMP, 1916; DE MAN, 1920). The differences proposed by ALCOCK and ANDERSON (1899a) between *P. media* and *P. propensalata* were actually based on the incorrect drawings given by BATE (1888), and later ALCOCK (1901) also suspected that the two species were perhaps identical. The type series of *P. media* is not in the Natural History Museum, London, and no reply has been obtained from the Indian Museum in Calcutta. Nevertheless, the descriptions and figures provided by ALCOCK and ANDERSON (1899a, b)

figures clearly show that the lateral sinuous ridges on abdominal tergites II and III are not interrupted (as well as in the other Indian specimens reported by KEMP, 1916) and CALMAN (in KEMP, 1916) also found that the types of *P. media* and *P. propensalata* are identical, I have little hesitation in following the previous authors in regarding these two species as synonyms.

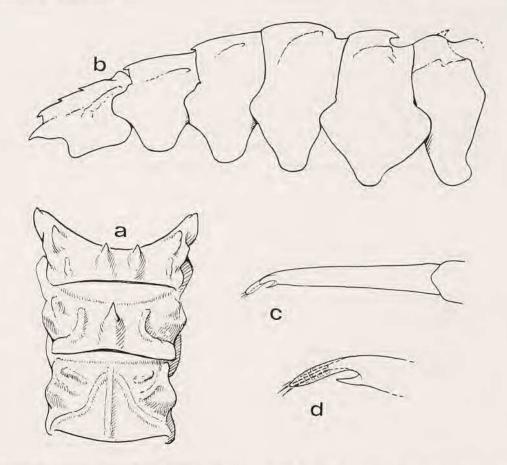


FIG. 7. — Pontocaris propensalata Bate, 1888 : a-b, ♂ type 10.7 mm, Kai Islands, "Challenger", stn 192, 256 m (BMNH-88.22) : a, dorsal view of abdominal tergites I-III; b, lateral view of abdomen. — c-d, ♀ (not ovigerous but in spawning molt) 11.7 mm, New Caledonia, MUSORSTOM 4, stn 171, 275-330 m (MNHN) : c, dactylus of pereiopod V; d, distal end of dactylus of pereiopod V.

LALITHA DEVI (1986) reported "P. pennata" from Kakinada, next to the Andaman Sea in the west of the Bay of Bengal. LALITHA DEVI's specimens may belong to the present species instead of P. pennata or P. affinis since the last three thoracic sternites are all sharply carinate medially in the males and the pereiopods II are not particularly lengthened in the ovigerous females of the Kakinadan specimens. Nevertheless, LALITHA DEVI's (1986) material was obtained from depths (10-40 m) much shallower than those known for P. propensalata (shallowest depth 100 m in the present study). Similarly, the Philippines "P. propensalata" specimens reported by CHACE (1984) from less than 60 m are actually P. hilarula. Moreover, CHACE's (1984) specimen from 349 m (USNM 205082) does not represent the present species but belongs to P. sibogae. The specimen reported by WHITELEGGE (1900) from S.W. Australia also needs to be verified.

CHACE (1984) defined the tip of the rostrum in this genus as cleft even though he had noticed that some specimens with an entire rostrum could be found in his "P. propensalata" (i.e. those from more than 60 m depth)

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and "P. sibogae" material. Most of the P. propensalata material in the present study has the rostrum entire. Occasionally the tip of the rostrum may be microscopically cleft (as in the type) and only in juveniles less than cl 5 mm are their rostrums always cleft. Moreover, in juveniles the rostrum (average cl 0.14 mm) and scaphocerite (average 1.75 times as long as broad) are generally longer, and the interlocking mechanism between the thoracic sternites and carapace has not yet developed. Although the tubercles of the lateral carapacial carina III are usually discernible and sometimes well-developed, this carina is virtually entire, with the anteriormost tubercle distinct only in some small males. Of the 86 specimens examined, only one specimen has a dorsolateral spine present on the abdominal somite V. The presence of the posterodistal tubercle on the abdominal pleuron IV is more variable, with 11 specimens (12.8%) bearing this tubercle on only one side of the pleuron while 11 others lack them completely.

Although no ovigerous female of this species has been obtained, two females (cl 11.3 mm and 12.4 mm) from the Philippines and another one from New Caledonia (cl 11.7 mm) are in the spawning molt. Their carpi of pereiopods II are still subequal to the chelae, but the dactyli of pereiopods V are noticeably modified. Moreover, slight modifications of the dactylus of pereiopod V are also observed in some of the large non-spawning females.

Although *Pontocaris* is not very well represented in New Caledonia and adjacent areas, *P. propensalata* is the dominant species of the genus in this region. This species is also common in Philippines waters.

#### Pontocaris profundior sp. nov.

Fig. 8

Aegeon pennata - BALSS, 1914b : 137 (? in part); 1915: 32 (? in part). Non Bate, 1888.

MATERIAL EXAMINED. — Holotype. Red Sea, Off Sudan, "Valdivia" 22, Medesa II, stn VA-22/II-99 TA, ser. no. 230, trawl with closing mechanism, 21°33'N, 38°21'E, 753-804 m, 9.4.1979 : 1 ovig. ♀ 7.8 mm (SMF).

**Paratypes. Red Sea.** Off Sudan, "Sonne" 2, Medesa I, trawl with closing mechanism : stn SO-02/25 TA, ser. no. ST201, 21°11.7'N, 37°26.8'E, 724-747 m, 15.10.1977 : 1  $\Im$  7.0 mm; 1 juv. 3.7 mm (SMF). — Stn SO-02/27 TA, ser. no. ST202, 21°10.7'N, 37°34'E, 733-757 m, 16.10.1977 : 3  $\Im$  4.5-6.1 mm; 2 ovig.  $\Im$  7.9-7.9 mm; 3  $\Im$  4.5-7.7 mm (SMF). — Stn SO-02/35 TA, ser. no. ST203, 20°52.5'N, 37°25.2'E, 588-490 m, 17.10.1977 : 4  $\Im$  6.0-7.1 mm; 6  $\Im$  4.9-7.9 mm; 3 juv. 4.7-5,0 mm (SMF). — Stn SO-02/36 TA, ser. no. ST204, 21°13.25'N, 37°15.9'E, 823-824 m, 17.10.1977 : 1 ovig.  $\Im$  7.6 mm; 1 juv. 4.4 mm (SMF). — Stn SO-02/58 TA, ser. no. ST213, 21°4.7'N, 37°54.5'E, 1310-1424 m, 22.10.1977 : 5  $\Im$  5.5-6.0 mm; 1 ovig.  $\Im$  8.9 mm; 19  $\Im$  5.5-10.2 mm (SMF). — Stn SO-02/66 TA, ser. no. ST214, 21°25.2'N, 37°45.2'E, 1043-1135 m, 23.10.1977 : 3  $\Im$  7.6-7.6 mm (SMF). — Stn SO-02/68 TA, ser. no. ST215, 21°25.8'N, 37°44.3'E, 1051-1134 m, 24.10.1977 : 1  $\Im$  5.5 mm; 4  $\Im$  5.5-7.4 mm (SMF).

"Valdivia" 22, Medesa II, trawl with closing mechanism : stn VA-22/II-99 TA, ser. no. 230, 21°33'N, 38°21'E, 753-804 m, 9.4.1979 : 4 ovig.  $\Im$  7.7-9.7 mm; 3  $\Im$  7.7-8.2 mm; 1 juv. 4.5 mm (SMF). — Stn VA-22/II-100 TA, ser. no. 231, 21°28.87'N, 38°15.37'E, 969-1110 m, 9.4.1979 : 1  $\Im$  5.2 mm; 1 ovig.  $\Im$  9.4 mm; 2  $\Im$  5.9 and 7.1 mm (SMF). — Stn VA-22/II-106 TA, ser. no. ST233, 21°19'N, 38°15.9'E, 1085-1121 m, 11.4.1979 : 1 ovig.  $\Im$  8.3 mm; 9  $\Im$  6.7-7.8 mm; 2 juv. about 4.6 mm (SMF). — Stn VA-22/II-111 TA, ser. no. ST235, 21°28.97'N, 38°15.55'E, 740-785 m, 12.4.1979 : 2  $\Im$  both 4.6 mm; 1 ovig.  $\Im$  9.5 mm; 4  $\Im$  6.2-7.2 mm; 1 juv. 3.8 mm (SMF). — Stn VA-22/II-121 TA, ser. no. 237, 21°26.5'N, 38°38.3'E, 779-801 m, 15.4.1979 : 2  $\Im$  5.5 and 7.6 mm; 1 juv. 4.2 mm (SMF). — Stn VA-22/II-122 TA, ser. no. ST238, 21°22'N, 39°4'E, 363-383 m, 17.4.1979 : 8  $\Im$  7.3-8.5 m; 5 ovig.  $\Im$  8.5-10.6 mm; 9  $\Im$  5.6-10.4 mm; 1 juv. 4.1 mm (SMF).

"Valdivia" 29, trawl with closing mechanism : stn VA 29/712 TA, ser. no. ST241, 21°17.4'N, 38°17.4'E, 712-1175 m,  $3/4.3.1981 : 1 \delta$  5.2 mm; 2  $\Im$  6.1 and 7.5 mm (SMF). — Stn 734 TA, ser. no. ST242, 24°40.5'N, 36°56.2'E, 712-745 m, 7.3.1981 : 1  $\delta$  4.7 mm; 2  $\Im$  5.7 and 5.8 mm (SMF).

"Meteor" cruise 5, beam trawl : stn 75, 22°53.8'N, 36°28.7'E, 748-845 m, 5.2.1987 : 1 & 6.3 mm; 2 ovig.  $\Im$  6.2 and 7.6 mm; 2  $\Im$  7.2 and 7.7 mm (SMF). — Stn 84, 22°52.5'N, 37°3.4'E, 880-884 m, 7.2.1987 : 1 & 5.1 mm; 1  $\Im$  7.3 mm; 1 juv. 3.4 mm (SMF). — Stn 85, 22°34.8'N, 36°45.9'E, 772-779 m, 7.2.1987 : 3 & 5.1-5.9 mm; 3 ovig.  $\Im$  6.0-8.3 mm; 5  $\Im$  5.7-8.0 mm; 4 juv. 3.7-5.5 mm (SMF). — Stn 90, 22°14.4'N, 37°44.7'E, 1095-1116 m, 8.2.1987 : 3 & 5.0-6.0 mm; 5  $\Im$  6.5-7.5 mm (SMF). — Stn 96, 22°4.2'N, 37°9.3'E, 600 m, 9.2.1987 : 1 & 6.0 mm; 2 ovig.  $\Im$  6.1 and 6.9 mm; 5  $\Im$  6.7-8.1 mm (SMF). — Stn 99, 22°8.4'N, 37°28.9'E, 827-863 m, 9.2.1987 : 2 & 4.9 and 5.1 mm; 3 ovig.  $\Im$  7.4-8.5 mm; 5  $\Im$  5.3-8.2 mm (SMF). — Stn 141, 19°56.1'N, 38°92'E, 807-863 m, 19.2.1987 : 1  $\Im$  8.8 mm (SMF). — Stn 148, 19°43.3'N, 37°40.2'E, 517-583 m, 20.2.1987 : 6 ovig.  $\Im$  6.4-7.6 mm; 11  $\Im$  5.1-7.9 mm (SMF). — Stn 149, 19°43.2'N, 37°40'E, 533-573 m, 20.2.1987 : 1  $\Im$  7.4 mm (SMF). — Stn 170, 18°47.4'N, 39°19.8'E, 857-1032 m, 23.2.1987 : 4  $\Im$ 

6.2-7.1 mm; 2 juv. 3.8 and 5.1 mm (SMF). — Stn 171, 18°34.5'N, 39°2.4'E, 434-469 m, 23.2.1987 : 4  $\eth$  5.5-6.4 mm; 3 ovig.  $\heartsuit$  6.9-9.3 mm; 6  $\heartsuit$  5.2-8.1 mm (SMF). — Stn 172, 18°34.7'N, 39°1.9'E, 428-459 m, 23.2.1987 : 5  $\circlearrowright$  4.9-5.9 mm; 1 ovig.  $\heartsuit$  8.2 mm; 13  $\heartsuit$  5.0-7.8 mm (SMF). — Stn 193, 19°24.3N, 38°30.9'E, 696-705 m, 28.2.1987 : 3  $\circlearrowright$  5.1-5.6 mm; 4 ovig.  $\heartsuit$  7.3-7.9 mm; 32  $\heartsuit$  5.3-9.3 mm (SMF). — Stn 194, 19°18.2'N, 38°14.8'E, 537-681 m, 28.2.1987 : 2  $\heartsuit$  6.8 and 10.1 mm (SMF).

Off Ras Burga, 29.5.1968 : 1 9 5.2 mm (SLR 1675, Decapoda 216, SMF, Hebrew University of Jerusalem in exchange).

Off Elat, 30.5.1968 : 2 9 4.52-5.05 mm (SLR 1713, Decapoda 225, SMF, Hebrew University of Jerusalem in exchange).

Off Nuweiba el Museina, : stn 31, beam trawl, 275-302 m, 8.10.1969 : 1 ovig. 9 7.3 mm, LEWINSOHN leg., NS 7210 (SMF, Tel-Aviv University in exchange).

Gulf of Aden. Off Yemen, "Meteor" cruise 5, beam trawl : stn 197, 19°52.2'N, 37°35.3'E, 747-778 m, 1.3.1987 : 3 ovig.  $\Im$  8.3-8.7 mm; 3  $\Im$  6.7-8.6 mm (SMF). — Stn 287, 12°16'N, 44°8.5'E, 472-479 m, 16.3.1987 : 3  $\Im$  7.3-7.6 mm; 1 ovig.  $\Im$  10.9 mm; 2  $\Im$  7.4 and 11.2 mm (SMF).

DESCRIPTION. — Body robust and somewhat dorsoventrally depressed. Integument hard. Eyes kidney-shaped. Rostrum 0.11-0.15 of carapace length, with tip usually cleft (rarely microscopically cleft or entire). Pair of lateral rostral teeth small but distinct. Carapace 1.14-1.43 times as long as wide; dorsal carina generally armed with 7-9 teeth; lateral carina I bearing 8-9 teeth, with anteriormost tooth somewhat separated from others; lateral carina II strongly interrupted by hepatic groove, bearing two teeth on anterior part and 5-8 teeth on posterior part; lateral carina III having 4-12 teeth (sometimes almost indistinguishable in small specimens). Scaphocerite about 0.19-0.3 carapacial length and 1.13-1.81 times as long as broad, with outer margin slight concave and distolateral tooth reaching or just exceeding distal margin of lamella.

Branchiostegal spine remarkably elongate and directed strongly outwards, far exceeding distolateral tooth of laterally extended scaphocerite. Pterygostomian spine much larger than antennal spine, well below and reaching far behind branchiostegal spine. Pereiopod II with carpus more or less as long as chela but becoming 1.35-1.61 times longer than latter in spawning females. Pereiopod III exceeding scaphocerite by 2/3-1 carpus; pereiopod IV by 1/2 propodus to dactylus. Pereiopod V overreaching scaphocerite by dactylus; with dactylus distinctly modified in spawning females: dactylus somewhat bifurcate; outer end armed with strong curved spine enveloped by a longer flap; inner lobe short, convex, laminate and slightly twisted. Thoracic sternite VI medially carinate, but low.

Abdominal sculpturing distinct and subdivided; bearing markedly elevated dorsal carinae on somites II to IV and pair of submedian carinae on somites I, V and VI. Anterior ends of dorsal and submedian carinae on abdominal somites I, II, and often III, developed into hooked teeth, posterior ends of dorsal and submedian carinae on somites IV to VI, and sometimes also III, sharply pointed. Lateral sinuous ridges interrupted on abdominal tergite II but continuous on tergite III. Usually one pair of dorsolateral spines present on abdominal somite V and two pairs on somite VI. Ventral margins of abdominal pleura all extremely elongate and acute. Abdominal pleuron I bearing elongate and acute anterobasal spine. Posterodistal tubercle absent on abdominal pleuron IV but a strong and elongate posterodistal spine often present on pleuron V. Telson spineless and longer than uropods. Eggs numerous and subspherical, with diameter of about 0.5 mm.

COLORATION. - Not known.

SIZE. - Largest female cl 11.2 mm and largest male cl 8.5 mm. Smallest ovigerous female cl 6.0 mm.

TYPE-LOCALITY. - Red Sea, off Sudan.

DISTRIBUTION. — Only known from the Red Sea and Gulf of Aden. At depths of 275-1424 m, mostly more than 400 m.

REMARKS. — The present species has a much deeper vertical distribution than the other species of the genus. The heavily "spiny" outline of *P. profundior* also makes it very distinct. The branchiostegal spine and the ventral teeth of the abdominal pleura are exceptionally long in this species. Moreover, the presence of a large hooked dorsal tooth on abdominal somite III and the abdominal pleuron I bearing an elongated anterobasal spine are also unique in the genus.

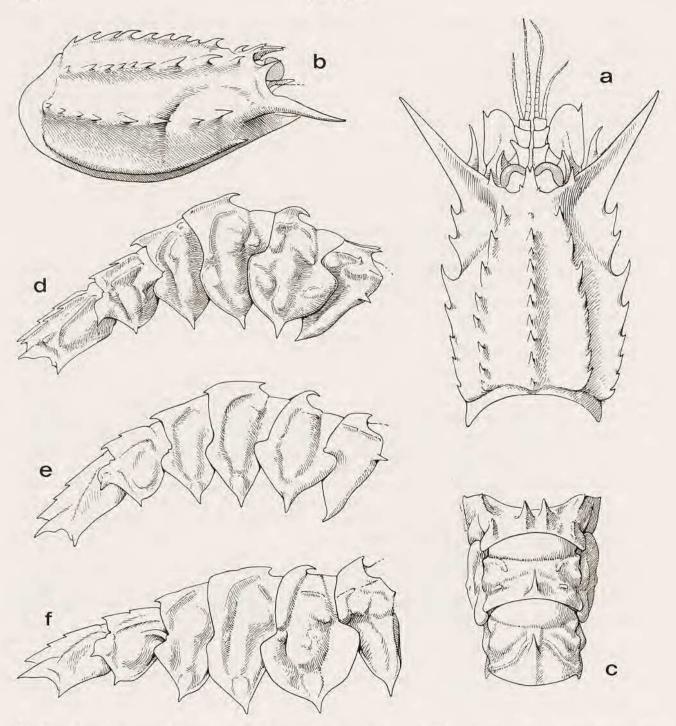


FIG. 8. — Pontocaris profundior sp. nov.: a-d, ovig. ♀ holotype 7.8 mm, Red Sea, off Sudan, "Valdivia" 22, Medesa II, stn VA-22/II-99 TA, 753-804 m (SMF) : a, dorsal view of carapace and anterior appendages; b, lateral view of carapace; c, dorsal view of abdominal tergites I-III; d, lateral abdomen. — e, ♀ paratype 7.5 mm, Red Sea, off Sudan, "Meteor", cruise 5, stn 172, 428-459 m (SMF) : lateral view of abdomen. — f, ovig. ♀ paratype 10.5 mm, Red Sea, off Sudan, "Valdivia" 22, Medesa II, stn VA-22/II-122 TA, 363-383 m (SMF) : lateral view of abdomen.

The abundant material from the Red Sea shows that *P. profundior* not only has a broad vertical distribution, but that there are also large variations in the development of the spines on the body. Generally, the spines on the

body and the dorsal tooth on abdominal tergite III tend to be less developed in material from shallower depths (also more often in males and juveniles). At one extreme, the anterior end of the dorsal carina on abdominal tergite III is nearly truncate (but still markedly elevated) and the posterodistal spine on abdominal pleuron V is absent. Since these variations can occur in material collected from both deep and shallow waters as well as from the same lot, it seems to be justifiable to treat all of them as the same species despite their large ranges of vertical distribution.

Other variations and aberrant conditions in this species are that 13 (4.5%) of the 286 specimens examined have entire rostrums and three specimens (1%) have only 5 or 6 dorsal teeth on the carapace. The number of dorsolateral spines on abdominal tergites V and VI are usually one and two pairs, respectively. However, rarely 0, 1, 3 or 4 dorsolateral spines may be present on abdominal tergite V and 0, 3, 5, 6 or 7 dorsolateral spines are found on abdominal tergite VI.

As in *P. affinis allodactylus*, also endemic to the Red Sea, both pereiopods II and V are modified in spawning females of *P. profundior*. Nevertheless, the "subchela" of pereiopod V is less developed and the carpus of pereiopod II is relatively shorter in spawning females of the present species.

ETYMOLOGY. — The occurrence of the present species in more than 1000 m depth is unusual for the genus and earns it the name *profundior*.

#### Pontocaris arafurae (Bruce, 1988)

Fig. 9

Pontocaris pennata Bate, 1888 : 499 (in part, male of the syntypes). Pontocheras arafurae Bruce, 1988 : 213, figs 1-6, 7A-E (type-locality : Arafura Sea). Pontocaris arafurae - HOLTHUIS, 1993, fig. 295.

MATERIAL EXAMINED. — Arafura Sea. "Aqua-Sam" : stn CP/92, off Orontes Reef, Port Essington, 11°4.5'S, 132°40'E, 15-22 m, 10-11.8.1986 : 1 ovig. ♀ 9.1 mm (holotype, NTM Cr.004127).

"Ausum" : stn HL 82-22, 10°58'S, 130°10'E, 27 m, 18.10.1982 : 1 9 7.9 mm (paratype, RMNH-D36756).

"Challenger" : stn 190, 8°56'S, 136°5'E, 90 m, 12.9.1874 : 1 & 6.7 mm (syntype of Pontocaris pennata Bate, 1888, NHM).

Indonesia. CORINDON 2 : stn 203, 1°08.6'S, 117°07.5'E, 25 m, 30.10.1980 : 1 ovig, ♀ 6.9 mm (MNHN-Na 5991). Chalutage, 6°22'S, 110°45'E, 10 m : 4 ♂ 5.9-7.5 mm (MNHN).

Philippines. MUSORSTOM 1 : stn 68, 13°58.8'N, 120°17.4'E, 183-199 m, 27.3.1976 : 1 ovig. ♀ 9.0 mm (MNHN-Na 5992).

**Thailand**. Gulf of Thailand near Nakon Sri Thammarat, no. 18, 21.7.1990 : 1 ovig. 28.1 mm; 327.9-8.8 mm, S. CHAITIAMVONG leg. (RMNH-D38352).

DIAGNOSIS. — Tip of rostrum pointed. Carapace about 1.23 (1.17-1.3) times as long as wide; dorsal carina armed with 8-9 rather low teeth; lateral carina I bearing 6-10 teeth and tubercles; lateral carina II bearing only one tooth on anterior part and two teeth on posterior part; lateral carina III not tuberculate and only pointed at anterior end; surface below lateral carina III somewhat eroded and reticulate. Scaphocerite about 1.57 (1.31-1.77) times as long as broad. Branchiostegal spine large but nearly straight, reaching 3/4-1 of outer margin of laterally extended scaphocerite. Pterygostomian spine smaller than antennal spine; well below and not quite reaching tip of branchiostegal spine. Pereiopod II with carpus only slightly longer (1.05-1.18 times) than chela, even in spawning females. Dactylus of pereiopod V strongly modified in spawning females: dactylus broadened and distally laminate; outer end bearing strong curved spine, enveloped by long flap and setae; lamella part convex and folded downwards. Thoracic sternite VI not carinate medially. Abdominal sculpturing rather eroded, with subdivisions poorly defined; lateral sinuous ridges interrupted on tergite II but continuous on tergite III. Abdominal somite IV lacking posteromedian spine. Usually one pair of dorsolateral spines present on abdominal somite V and two pairs on somite VI. Ventral margins of abdominal pleura generally acute, except that of pleuron V somewhat truncate in males. Posterodistal tubercle sometimes present on abdominal pleuron V, absent on pleuron IV. Eggs numerous and subspherical, with diameter of about 0.35 mm.

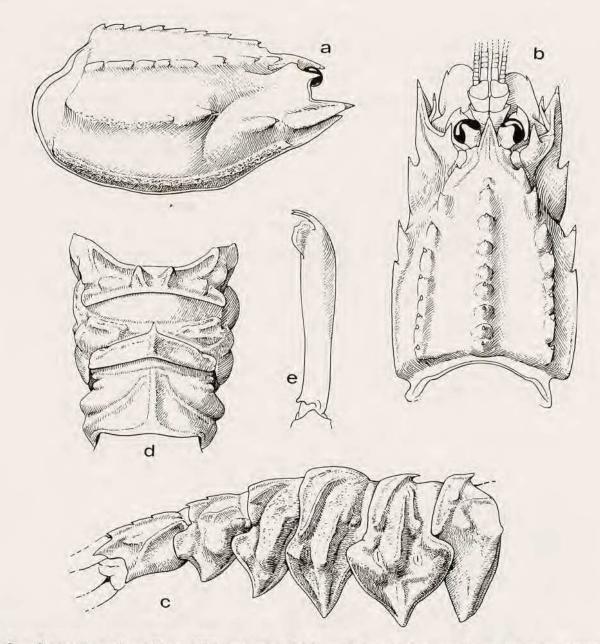


FIG. 9. — Pontocaris arafurae (Bruce, 1888) : a-e, ovig. ♀ 6.9 mm, Indonesia, CORINDON 2, stn 203, 25 m (MNHN-Na 5991) : a, lateral view of carapace and anterior appendages; b, dorsal view of carapace and anterior appendages; c, lateral view of abdomen; d, dorsal view of abdominal tergites I-III; e, dactylus of pereiopod V.

COLORATION. — Reported by BRUCE (1988) as "Overall opaque chalky white, with median and dorsolateral carapacial spines and tubercles orangish, median and oblique ridges orangish, uropods white; branchiostegite and pleura porcelain white; pereiopods and pleopods pinkish; ova bright orange."

SIZE. — Rather small, largest female cl 9.1 mm and largest male cl 7.5 mm. Smallest female at spawning molt cl 6.9 mm (ovigerous).

DISTRIBUTION. - Arafura Sea to Indonesia, the Philippines and Thailand, at depths of 10-199 m.

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REMARKS. - The present species is unique in the genus by lacking a posteromedian spine on the abdominal somite IV (though the posteromedian part of abdominal somite IV is slightly protruded in two non-spawning females from Thailand) and having the surface below lateral carina III of the carapace eroded and reticulate. Both BATE (1888) and CALMAN (in KEMP, 1916) had noticed that the male in the syntypes of P. pennata is rather different from the females in having an entire rostrum and smoother abdominal sculpturing. BATE's (1888) types shows that his male actually represents the present form and is not conspecific with the two females. On the other hand, the recently described species Pontocheras arafurae Bruce, 1988, from a nearby locality closely resembles BATE's (1888) male. Although slight differences are found in the figures provided by BRUCE (1988, figs 1-2), an examination of the holotype and a paratype of Pontocheras arafurae reveals that it belongs to the same species as BATE's (1888) male. The differences in BRUCE's (1988) figures are mostly due to inexact representation : the posterior part of lateral carapacial carina II should have two teeth instead of one and no other tooth except the one at the anterior end is present on the lateral carapacial carina III. The dorsal carina on abdominal somite II is rather low in the holotype but is not completely absent as in BRUCE's (1988) figure. Nevertheless, the network-like markings on the ventral surface of the carapace are rather obscure in the holotype (but distinct in the paratype). Since the larger female in BATE's (1888) type series is now chosen as the lectotype of P. pennata (see "Remarks" under P. pennata), BRUCE's (1988) name can be retained for the present form.

The anterior part of the lateral carapacial carina II bears only one tooth in the present species. Such a condition only rarely occurs on one side of the carapace in the other species of the genus (e.g. *P. propensalata, P. hilarula, P. major, P. laurentae* and *P. pennata*). Only in the smaller female of the syntypes of *P. pennata* are both sides of the anterior part of the lateral carapacial carina II armed with a tooth. Furthermore, the teeth on the body and the abdominal sculpturing are sometimes rather eroded in the present species. The already minute lateral rostral teeth are often very obscure and the ventral margins of the abdominal pleura are less acute in the males.

## Pontocaris hilarula (de Man, 1918)

Fig. 10

Aegeon propensalata var. hilarula de Man, 1918 : 301 (type-locality : Lesser Sunda Islands, Indonesia); 1920 : 296, pl. 24 figs 71-71f.

Pontocaris propensalata - CHACE. 1984 : 43 (in part). Non Bate, 1888.

MATERIAL EXAMINED. — Philippines. "Albatross" : stn 5104, 14°45'48"N, 120°12'20"E, 60 m, 8.01.1908 : 1 & 6.5 mm; 5 & 5.9-8.6 mm (USNM 205081). — Stn 5131, 7°35'N, 122°07'E, 49 m, 6.02.1908 : 3 & 6.2-6.8 mm (USNM 205079). — Stn 5257, 7°22'12"N, 124°12'15"E, 51 m, 22.05.1908 : 1 & 6.3 mm (USNM 205080).

Indonesia. "Siboga": stn 47, Bay of Bima, near south fort, 55 m, 8.12.1899 : 1 & 6.8 mm (type, ZMA).

New Caledonia. LAGON : stn 142, 22°20'S, 166°50'E, 34 m, 24.8.1984 : 1 ♂ 6.9 mm (MNHN). — Stn 833, 20°49.8'S, 165°17.7'E, 52-70 m, 11.1.1987 : 1 ♀ 5.6 mm (MNHN).

DIAGNOSIS. — Tip of rostrum distinctly cleft. Carapace about 1.12-1.22 times as long as wide; dorsal carina bearing 8-9 low teeth, lateral carina I provided with 8-10 blunt tubercles; lateral carina II generally having two low and obtuse teeth on anterior part and 5-7 flattened tubercles on posterior part; lateral carina III with 10-12 flattened tubercles. Scaphocerite about 1.25-1.44 times as long as broad. Branchiostegal spine large but straight, bending only slightly outwards and downwards at tip, nearly reaching to just exceeding 1/2 along outer margin of laterally extended scaphocerite. Pterygostomian spine as large as antennal spine, situated well below it and more or less reaching tip of branchiostegal spine. Pereiopod II with carpus about as long as chela (0.94-1.08), even in spawning females. Dactylus of pereiopod V strongly modified in spawning females : broadened and distally laminate; outer end bearing a strong curved spine, enveloped by a long flap; lamella part convex and strongly folded downwards. Thoracic sternite VI medially elevated into a low but distinct triangular plate. Abdominal sculpturing distinct and subdivided; lateral sinuous ridges on abdominal tergite II interrupted, those on tergite III dorsally continuous but usually interrupted near lateral ends. Strong posteromedian spine present on abdominal somite IV. Abdominal somite VI armed with 2-4 dorsolateral spines but none on somite V. Abdominal pleura ventrally truncate, sometimes round in large females. Abdominal pleura V and often IV with posterodistal margin slightly angular.

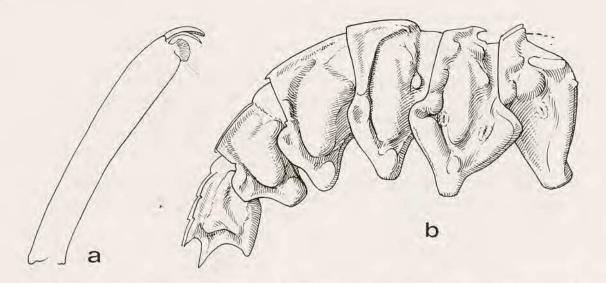


FIG. 10. — Pontocaris hilarula (de Man, 1918) : a, ♀ (not ovigerous but in spawning molt) 8,6 mm, Philippines, "Albatross", stn 5104, 60 m (USNM 205081) : dactylus of pereiopod 5. — b, ♂ 6.9 mm, New Caledonia, Ouen Island, Prony Bay, LAGON, stn 142, 34 m (MNHN) : lateral view of abdomen.

COLORATION. - Not known.

SIZE. — Largest male cl 6.9 mm and largest female cl 8.6 mm. Smallest female at spawning molt cl 7.7 mm.

DISTRIBUTION. — Only known with certainty from the Philippines, Indonesia and New Caledonia, at depths of 34-70 m.

REMARKS. — The present form is unique in that all the carinae on the carapace bear distinct, but low, obtuse tubercles. In the other species, such as *P. pennata* and *P. arafurae* where the lateral carapacial carinae are nearly smooth, the anterior ends of the lateral carinae II (both the anterior and posterior parts) and III are still sharply pointed. However, the anterior ends of the lateral carapacial carinae II and III all terminate in round, obtuse teeth in *P. hilarula*, except for spawning females. Also different from the other species of the genus are the lateral sinuous ridges on abdominal tergite III which, though continuous dorsally, are generally interrupted near the lateral ends. Only in one of the 13 specimens examined is the lateral sinuous ridge on abdominal tergite III continuous along its entire length. The characters used by DE MAN (1920) to separate this form from the typical *P. propensalata*, such as the cleft rostrum and the lateral sinuous ridges interrupted at the abdominal tergite II, are now found to be very constant. Therefore, DE MAN's (1918) variety should warrant full specific status, in contrast to the opinion of CHACE (1984). A re-examination of CHACE's (1984) specimens shows that both *P. hilarula* (all those from less than 60 m deep) and *P. sibogae* are present in the "*Albatross*" Philippine material.

The materials from the different localities are very similar, except for the branchiostegal spine being straighter in the type. The abdominal pleura of the female are slightly less truncate and may even be somewhat rounded. Although no ovigerous female of the present species has been obtained, three females (cl 7.7-8.6 mm) from the "Albatross" collection are in the spawning molt. Their carpi of pereiopods II are subequal to the chelae and the dactyli of pereiopods V are strongly modified (with a shape very similar to that of *P. arafurae*).

#### Pontocaris affinis affinis (Alcock, 1901)

Fig. 11

Aegeon affine Alcock, 1901 : 118 (type-locality : Bombay). — ALCOCK & MCARDLE, 1901 : pl. 51 figs 3-3a, 4. Aegeon pennata var. affinis - DE MAN, 1920 : 292.

Pontocaris pennata - HOLTHUIS, 1980 : 152 (in part). Non Bate, 1888.

? Aegeon pennata - KEMP, 1916 : 376 (in part, material from India). Non Bate, 1888.

? Pontocaris pennata - SANKOLLI & SHENOY, 1979 : 62. Non Bate, 1888.

MATERIAL EXAMINED. — India (Bombay). "Investigator" : stn 242, 8.9.1915 (date probably labeled wrong) : 1  $\stackrel{\circ}{\sigma}$  7.9 mm; 1 ovig.  $\stackrel{\circ}{\varphi}$  10.0 mm (syntypes, NHM). — 17°27'N, 71°41'E, 102-106 m : 6  $\stackrel{\circ}{\varphi}$  6.0-7.8 mm, Reg. no. : 3424-9/10 [part of ALCOCK's (1901) specimens] (MNHN-Na 4713). — No date, 102-106 m : 1 ovig.  $\stackrel{\circ}{\varphi}$  9.8 mm (very likely from the same station as the preceding one, MNHN-Na 1172).

Bay of Bengal. "Lady Fraser", sand heads, mouth of river Hooghly, 2.3.1928 : 2 9 9.1 and 10.3 mm, Reg. no. C4011/1 (MNHN-Na 4715).

Madagascar. "FAO 60" : stn 73/90, Morombe, 21°51'S, 43°10'E, 160 m, 9.8.1973 : 1 2 11.3 mm (MNHN).

"Vauban" : stn CH 130, 15°20'S, 46°1.5'E, 170-175 m, 19.1.1975 : 1 ovig. 9 11.0 mm; 1 9 11.5 mm (MNHN).

DIAGNOSIS. — Tip of rostrum distinctly cleft. Carapace about 1.21 (1.14-1.27) times as long as wide; dorsal carina bearing 8-10 teeth; lateral carina I armed with 8-10 (mostly 9-10) teeth; lateral carina II having two teeth on anterior part and 4-7 teeth or tubercles on posterior part; lateral carina III with 1-11 sometimes barely distinguishable tubercles. Scaphocerite about 1.48 (1.44-1.52) times as long as broad. Branchiostegal spine large and wing-like, directed slightly to moderately outwards, extending over 3/4-1 of outer margin of laterally extended scaphocerite. Pterygostomian spine slightly larger than antennal spine and generally failing to reach tip of branchiostegal spine, situated below or on same level with latter spine. Pereiopod II considerably lengthened in spawning females and with carpus 1.41-1.8 (average 1.61) times longer than chela, but dactylus of pereiopod V remaining simple. Thoracic sternite VI medially elevated into triangular plate but not very high or hooked. Abdominal sculpturing distinct and subdivided, lateral sinuous ridges on abdominal tergite II interrupted but continuous on tergite III. Abdominal somite IV bearing strong posteromedian spine. Usually one pair of dorsolateral spines present on abdominal somite V and two pairs on somite VI. Abdominal pleura ventrally acute. Abdominal pleuron IV occasionally (21.4%) with one side having posterodistal tubercle but none at pleuron V. Eggs numerous and subspherical, about 0.5 mm in diameter.

COLORATION. — Not known, though KEMP (1916) stated that his Indian material was "grey, touched with dark brown and green marks" or "irregularly banded with lichen green and mottled pink".

SIZE. — Largest female cl 11.5 mm and smallest spawning female cl 9.1 mm. The only male from the syntypes is cl 7.9 mm (largest cl 9 mm in ALCOCK, 1901).

DISTRIBUTION. — Indian Ocean, but only known with certainty from Bombay, Bay of Bengal and Madagascar, at depths of 102 (maybe much shallower, see "Remarks") -175 m.

REMARKS. — The present species was always thought to be related to *P. pennata*. DE MAN (1920) treated it as a subspecies of the latter and HOLTHUIS (1980) tentatively synonymized the two names. CALMAN (in KEMP, 1916) examined the types of the two species and believed that they were identical. KEMP (1916) came to a similar conclusion after having compared his Indian material with a syntype of *Aegeon obsoletum* Balss, 1914, from Japan. By arguing that there is no difference in the lengths of the pereiopods II between the sexes in the Kakinada Bay material, LALITHA DEVI (1986) claimed that *P. affinis* should be treated as a junior synonym of *P. pennata*.

However, the present study found that ALCOCK's (1901) species is actually very different from *P. pennata* by the lateral sinuous ridges on abdominal tergite III being continuous instead of interrupted. Moreover, 6 spawning females (three ovigerous, including one or probably two of the syntypes) still have intact pereiopods II and their carpi are 1.41-1.8 times longer than the chelae and extend to the tips of pereiopods I. In the male and the young females the carpi of the pereiopods II are only slightly longer than the chela and do not reach the middle of the subchelae of pereiopods I (also see ALCOCK & MCARDLE, 1901, figs 3-3a, 4; DE MAN, 1920 : 295). Thus, it can be concluded that the carpus of pereiopod II lengthens considerably when females molt for spawning, a peculiar phenomena so far only known in the present species, *P. sibogae* and *P. profundior*. The ovigerous female syntype from the Natural History Museum, London, has the pereiopod V missing. Nevertheless, an intact pereiopod V is present in an another ovigerous female from the type-locality (MNHN-Na 1172, highly likely to also be from the

type series) and the dactylus is simple and without any modification. A similar situation is also present in the pereiopod V of an ovigerous female from Madagascar. With such significant differences, the name *affinis* is revived and warrants full specific status.

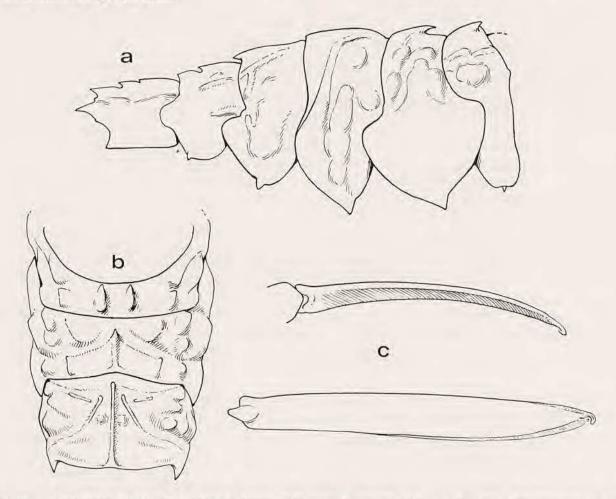


FIG. 11. — Pontocaris affinis affinis (Alcock, 1901) : a-b, ovig. ♀ syntype 10.0 mm, Bombay, "Investigator", stn 242 (BMNH) : a, lateral abdomen; b, dorsal view of abdominal tergites I-III. — c, ovig. ♀ (? syntype) 9.8 mm, Bombay, 102-106 m (MNHN-Na 1172) : dactylus of pereiopod V.

The differences noticed by DE MAN (1920) on the thoracic sternites between *P. affinis* and *P. pennata* also warrant special attention. Although the carination on the middle of the last two thoracic sternites is variable according to the different stages of the females, the middle of thoracic sternite VI is always distinctly carinate in *P. affinis* but smooth in *P. pennata*. On the other hand, ALCOCK (1901) rightly stated that the last three thoracic sternites are more strongly carinate in *P. propensalata* (Aegeon medium in ALCOCK, 1901) than in *P. affinis*. The median carina on thoracic sternite VI is hooked in the former, but only triangular in the latter.

All 14 specimens examined here have the rostrum distinctly cleft. The ventral margins of the abdominal pleura are generally acute, except that of pleuron V which is somewhat round in the male. Although the tubercles on lateral carapacial carina III are often poorly defined, it appears that the number of tubercles is somewhat higher in the Madagascan material (7-11) than in that from India (1-9). Furthermore, two of the three Madagascan specimens have the dorsal spine wanting on one of the dorsolateral carinae of abdominal somite V. On the other hand, only one small female from Bombay has one instead of two dorsal spines on one of the dorsolateral carinae of abdominal somite VI.

## ON THE GENERA AEGAEON, PONTOCARIS AND PARAPONTOCARIS

Although *P. affinis* is the dominant species in the Indian Ocean, a re-examination of the *Pontocaris* material reported by KEMP (1916, some came from only 12 fathoms or 22 m), SANKOLLI and SHENOY (1979, collected from 33-46 m) and LALITHA DEVI (1986) from India and the Arabian Sea (including the Persian Gulf) is necessary to determine their exact identities.

## Pontocaris affinis allodactylus subsp. nov.

Fig. 12

Aegeon pennata - BALSS, 1914b : 137 (? in part); 1915 : 32 (? in part). — KEMP, 1916 : 376 (? in part, those from the Partagairs parts from the Part

Pontocaris pennata - HOLTHUIS, 1980 : 152 (in part). Non Bate, 1888.

MATERIAL EXAMINED. — Holotype. Red Sea. North of Massawa Channel, 9.12.1957 : 1 ovig. 9 9.1 mm, A. BEN-TUVIA leg., Nr. E57/513 (RMNH-D42362).

Paratypes. Red Sea, North of Massawa Channel, 9.12.1957 : 3 ♂ 6.2-6.4 mm; 1 ovig. ♀ 7.1 mm; 9 ♀ 6.3-8.1 mm, A. BEN-TUVIA leg., Nr. E57/513 (RMNH-D42363).

Other material. Red Sea. "Negus Salomon" : stn 7, 15°32.3'N, 40°23'E, beam trawl, 110 m, 19.10.1965 : 51 juv. 3.5-5.7 mm, ISRSE no. 1332 (RMNH-D42365, D42368, D42369). — Stn 8, 15°32'N, 40°17'E, beam trawl, 9-11 m, 22 10 1965 : 1.9, 65 mm; 2 inv 52 and 58 mm; 10055

11 m, 22.10.1965 : 1 \u2262 6.5 mm; 2 juv. 5.2 and 5.8 mm, ISRSE no. 1671 (RMNH-D42634). North of Marsat, Abu Samra, 26°16.5'N, 34°47'E, 604 m, 30.5.1968 : 1 juv. 4.3 mm, SLR 1699, Decapoda 222 (RMNH-D42366).

Locality unknown : 1 juv. 4.7 mm, ISRSE 1965, no. 3549 (RMNH-D42367).

DIAGNOSIS. — The Red Sea material is almost identical with the P. affinis specimens from Madagascar except :

Spawning females with pereiopod II considerably lengthened and dactylus of pereiopod V strongly modified: carpus of pereiopod II 1.63 times longer than chela while dactylus of pereiopod V is distally laminate, somewhat twisted and convex, outer end provided with long curved flap;

Cleft of rostrum less distinct, even microscopically cleft in one specimen;

Branchiostegal spine slightly longer and generally extending to tip of distolateral tooth of laterally extended scaphocerite;

Median carina of abdominal tergite III sometimes rather indistinct.



FIG. 12. — Pontocaris affinis allodactylus subsp. nov., ovig. ♀ holotype 9.1 mm, Red Sea, North of Massawa Channel (RMNH-D42362) : distal end of dactylus of pereiopod V. COLORATION. - Not known.

SIZE. — Largest female cl 9.1 mm (ovigerous) and largest male cl 6.4 mm. Smallest spawning female cl 6.7 mm.

TYPE-LOCALITY. — Red Sea, north of Massawa Channel.

DISTRIBUTION. — Only known with certainty from the Red Sea, at depths of 9-604 m (see "Remarks") on bottoms of light brown soft mud with few fragments and large particles.

REMARKS. — Although the general appearance of the Red Sea form is almost identical with the *P. affinis* material of the other localities, it differs dramatically from most of the other species of the genus in having both the pereiopods II and V distinctly modified in spawning females. However, of the 70 specimens examined in the present study, 55 are juveniles and 11 others are males and non-spawning females. The carpus of pereiopod II is only very slightly longer than the chela in males and juveniles. Thus, it is nearly impossible to distinguish most of the present Red Sea specimens from the other *P. affinis* material. In view of such difficulties, a subspecific

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rather than a full specific status is assigned to the Red Sea form for the time being. Perhaps some other differences in morphology or coloration will be found later to separate this form more effectively.

It is worth noting that the ability to modify the dactylus of pereiopod V in spawning females may align the present form with *P. major* and *P. laurentae*. In addition to the carpus of the pereiopod II being considerably lengthened in spawning females, the abdominal somite V generally bears a pair of dorsolateral spines in *P. affinis allodactylus* (though in two specimens there is only one dorsolateral spine). *P. affinis allodactylus* can also be distinguished from the above two species by the nearly smooth lateral carapacial carina III and the abdominal somite V lacking a posterodistal tubercle.

The vertical distribution of the present material is from 9 to 604 m. These data, however, are all from juvenile specimens and a non-spawning female. The lot containing the holotype and the other spawning females lacks data on depth. As mentioned above, the juveniles of the present subspecies are almost indistinguishable from the nominate subspecies. Although unlikely, this leaves the possibility that *P. affinis affinis* may also occur in the Red Sea.

ETYMOLOGY. — The Greek *alloios* and *dactylus* refers to the strongly modified dactylus of the pereiopod V in the spawning females of the Red Sea material, as compared with the simple dactylus in the nominate subspecies.

#### Pontocaris major sp. nov.

Fig. 13

Pontocaris sibogae - CHACE, 1984 : 44 (in part). Non de Man, 1918.

MATERIAL EXAMINED. — Holotype. Philippines. MUSORSTOM 1 : stn 36, 14°0.3'N, 120°17'E, 187-210 m, 23.3.1976 : 1  $\Im$  20.3 mm (not ovigerous but in spawning molt, MNHN).

**Paratypes.** Philippines. "Albatross" : stn 5117, 13°52'22"N, 120°46'22"E, 216 m, 21.12.1908 : 3 & 14.3-15.2 mm (USNM 205069). — Stn 5183, 10°32'48"N, 122°26'E, 351-457 m, 30.3.1908 : 1 & 13.2 mm (USNM 205071). — Stn 5194, 11°15'30"N, 124°11'E, 271 m, 3.4.1908 : 1 & 14.9 mm (USNM 205070). — Stn 5247, 7°02'N, 125°38'45"E, 247 m, 18.5.1908 : 5 & 12.3-13.9 mm; 3 ovig. &pi 16.0-17.7 mm; 7 &pi 11.4-17.6 mm (USNM 205067). — Stn 5255, 7°03'N, 125°39'E, 247 m, 18.5.1908 : 1 ovig. &pi 15.2 mm (USNM 205068). — Stn 5272, 14°N, 120°22'30"E, 216 m, 14.7.1908 : 1 &pi 17.0 mm (USNM 205066). — Stn 5369, 13°48'N, 121°43'E, 194 m, 24.2.1909 : 1 &pi 12.2 mm (USNM 205065). — Stn 5393, 12°03'30"N, 124°03'36"E, 249 m, 13.3.1909 : 2 &pi 11.5 and 14.0 mm (USNM 205064). — Stn 5394, 12°00'30"N, 124°05'36"E, 280 m, 13.3.1919 : 1 &pi 11.4 mm (USNM 205062). — Stn 5396, 11°57'N, 124°12'24"E, 251 m, 15.03.1909 : 4 &pi 13.3-14.4 mm (USNM 205074). — Stn 5397, 11°57'27"N, 124°10'42"E, 245 m, 15.3.1909 : 1 &pi 13.8 mm (USNM 205073).

MUSORSTOM 1 : stn 7, 14°0.2'N, 120°18.2'E, 185-200 m, 19.3.1976 : 1 & 10.9 mm (MNHN-Na 5974). — Stn 10, 13°59.8'N, 120°18.2'E, 187-205 m, 19.3.1976 : 1 & 12.1 mm; 1  $\Im$  6.4 mm (MNHN). — Stn 12, 14°0.5'N, 120°17.2'E, 187-210 m, 20.3.1976 : 1 & 9.6 mm (MNHN-Na 5975). — Stn 24, 14°00.0'N, 120°18.0'E, 189-209 m, 22.3.1976 : 3 & 10.2-11.8 mm; 2  $\Im$  15.7-17.7 mm (MNHN-Na 5990). — Stn 25, 14°02.7'N, 120°20.3'E, 191-200 m, 22.3.1976 : 3 & 11.6-14.5 mm (MNHN-Na 5978). — Stn 36, 14°01.2'N, 120°20.2'E, 187-210 m, 23.3.1976 : 4 & 11.4-16.0 mm; 3  $\Im$  20.9-21.3 mm (MNHN-Na 5988). — Stn 42, 13°55.1'N, 120°28.6'E, 379-407 m, 24.3.1976 : 1  $\Im$  13.8 mm (MNHN-Na 5979).

MUSORSTOM 2 : stn 41, 13°16.9'N, 122°46.6'E, 166-172 m, 25.11.1980 : 2 & 9.9 and 11.6 mm (MNHN-Na 5976). — Stn 66, 14°00.6'N, 120°20.3'E, 192-209 m, 29.11.1980 : 2 & 8.1 and 8.9 mm; 1 ovig,  $\Im$  16.8 mm (MNHN-Na 5977).

MUSORSTOM 3 : stn 100, 14°N, 120°18'E, 189-199 m, 1.6.1985 : 1  $\Im$  5.5 mm (MNHN). — Stn 101, 14°00.1'N, 120°19.2'E, 194-196 m, 1.6.1985 : 1  $\Im$  13.9 mm (MNHN). — Stn 108, 14°01.1'N, 120°17.9'E, 188-195 m, 2.6.1985 : 1  $\Im$  6.8 mm (MNHN). — Stn 120, 12°05.6'N, 121°15.6'E, 219-220 m, 3.6.1985 : 2  $\Im$  6.8 and 19.7 mm (MNHN).

DESCRIPTION. — Body large, robust and somewhat depressed dorsoventrally. Integument hard. Eyes kidney shaped. Rostrum about 0.12 (0.11-0.14) times carapacial length, tip varying from entire (only in males) to microscopically cleft. Pair of lateral rostral teeth small but distinct. Carapace about 1.25 (1.15-1.32) times as long as wide; dorsal carina armed with 9-10 teeth; lateral carina I having 8-10 teeth; lateral carina II strongly interrupted by hepatic groove, usually bearing two teeth on anterior part and 6-9 teeth and tubercles on posterior part; lateral carina III provided with 11-17 teeth and tubercles. Scaphocerite about 1.26 (1.16-1.36) times as long as broad, with distolateral tooth well behind (in large specimens) or reaching distal margin of lamella.

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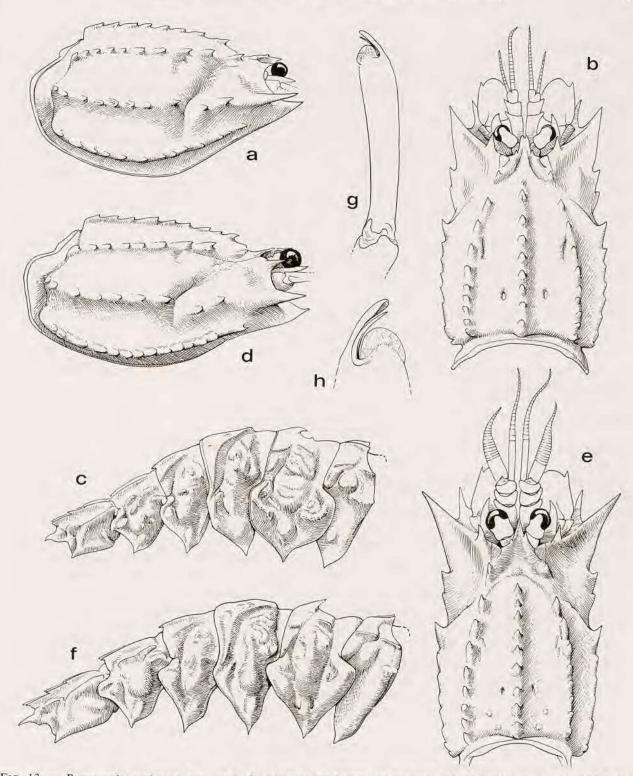


FIG. 13. — Pontocaris major sp. nov.: a-c, ♀ holotype 20.3 mm, Philippines, MUSORSTOM 1, stn 36, 187-210 m (MNHN): a, lateral view of carapace; b, dorsal view of carapace and anterior appendages; c, lateral view of abdomen. — d-f, ♂ paratype 11.6 mm cl. Philippines, MUSORSTOM 1, stn 25, 191-200 m (MNHN-Na 5978): d, lateral view of carapace; e, dorsal view of carapace and anterior appendages; f, lateral view of abdomen. — g-h, ♀ (not ovigerous but in spawning molt) paratype 21.3 mm (MNHN-Na 5988), Philippines, MUSORSTOM 1, stn 36, 187-210 m : g, dactylus of pereiopod V; h, distal end of dactylus of pereiopod V.

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Branchiostegal spine large and wing-like; directed strongly outwards in young but less so in large specimens and sometimes even almost straight in spawning females; extending beyond or reaching 2/3-1 (in large specimens) of outer margin of laterally extended scaphocerite. Pterygostomian spine much larger than antennal spine, well below and either not reaching as far as or overreaching (in spawning females), tip of branchiostegal spine. Pereiopod I exceeding scaphocerite by entire subchela. Pereiopod II overreaching scaphocerite by about half of chela, with carpus only slightly longer (1.07-1.24; avg. 1.14) than chela, even in spawning females. Pereiopod II exceeding scaphocerite by 1/2-2/3 carpus; pereiopod IV by entire dactylus to 1/3 propodus. Pereiopod V exceeding scaphocerite by 1/2-1 dactylus, with dactylus strongly modified and paddle shaped in spawning females : distal part of dactylus forming a thin lamellar plate and slightly twisted, distal margin convex, outer end notched and bearing a strong, curved spine, accompanied by longer lamellar hood and setae. Thoracic sternite VI armed with large, hooked median tooth.

Abdominal sculpturing distinct and subdivided. Abdomen bearing dorsal carinae on somites II to IV and pair of submedian carinae on somites I, V and VI. Anterior ends of dorsal and submedian carinae on abdominal somites I and II developed into large teeth, posterior ends of dorsal and submedian carinae on somites IV to VI sharply pointed. Lateral sinuous ridges interrupted on abdominal tergite II, but continuous on tergite III. Generally two pairs of dorsolateral spines present on abdominal somite VI, but none on somite V. Ventral margins of abdominal pleura all elongate and acute. Posterodistal tubercle absent on abdominal pleuron IV but sometimes present on pleuron V. Telson spineless and longer than uropods. Eggs numerous and subspherical, diameter about 0.4 mm.

COLORATION. - Not known.

SIZE. — Largest species of the genus, with females attaining a length of cl 21.3 mm and males cl 16.0 mm. Smallest spawning female cl 15.2 mm.

TYPE-LOCALITY. - The Philippines.

DISTRIBUTION. - Only known in the Philippines, at depths of 116-457 m, but generally less than 280 m.

REMARKS. — The size of this species is exceptionally large for Pontocaris; the largest P. sibogae just attains the spawning size of P. major. The present form can be easily mistaken for DE MAN's (1918) Aegeon sibogae var. intermedia, which has the lateral sinuous ridges on abdominal tergite III continuous. However, a re-examination of DE MAN's (1918) type from Indonesia reveals that it differs significantly from the Philippine material in having the ventral margins of the abdominal pleura only slightly pointed and not at all elongate. Furthermore, a welldeveloped posterodistal tubercle is present on both sides of abdominal pleuron IV in DE MAN's specimen. Most importantly, the type of Aegeon sibogae var. intermedia has one pereiopod II still intact and the carpus is 1.42 times longer than the chela (also see DE MAN, 1920). In the Philippine form, however, the carpus of pereiopod II is always subequal to the chela in both sexes and in females at different stages. Although DE MAN's (1918) type is a non-spawning female and has the dactylus of pereiopod V simple, its considerably lengthened pereiopod II (as often occurs in large non-spawning females of P. sibogae) and the above characteristics indicate that the continuous lateral ridges on abdominal tergite III of Aegeon sibogae var. intermedia is merely one of the large variations exhibited in P. sibogae (for more details see "Remarks" under P. sibogae). Therefore, DE MAN's (1918) name cannot be applied to the present material and a new name should be used for this Philippine form. As suspected, the Philippine "Albatross" material, reported as "P. sibogae" by CHACE (1984), contains P. sibogae and P. major.

Unlike *P. sibogae*, the morphological characters of the present species are rather constant. Besides the lateral sinuous ridges on abdominal tergite III always being continuous (interrupted on one side in one specimen), all 73 specimens examined lack a posterodistal tubercle on the abdominal pleuron IV. Furthermore, the abdominal somite V bears 1-2 dorsolateral spines in only five specimens (6.8%). The tip of the rostrum varies from cleft to entire (mostly) in the males of this species. However, no female with an entire rostrum was found, though their tips are often microscopically cleft. Besides the fact that the dactylus of pereiopod V is strongly modified in

spawning females of the present species, this dactylus may be variably modified even in large non-spawning females and, occasionally, also slightly transformed in large males.

The difference in the shape of the branchiostegal spine is much more pronounced with age than between sexes in *P. major*. The branchiostegal spine, directed strongly outward in small specimens, becomes nearly straight in some spawning females, making the latter look rather different to the former. Nevertheless, the ventral margins of the abdominal pleura are always elongate and acute in specimens of all ages and sexes.

ETYMOLOGY. — The name major refers to the large size of this species.

# Pontocaris laurentae sp. nov.

Fig. 14

MATERIAL EXAMINED. — Holotype. Indonesia (Makassar Strait). CORINDON 2 : stn 267, 1°56.6'S. 119°16.7'E, 134-186 m, 7.11.1980 : 1 2 12.6 mm (not ovigerous, but in spawning molt, MNHN-Na 12935).

**Paratypes. Indonesia** (Makassar Strait). CORINDON 2 : stn 208, 0°14.6'S, 117°52.0'E, 150 m, 31.10.1980 : 1 ♀ 12.9 mm (MNHN-Na 5982). — Stn 267, 1°56.6'S, 119°16.7'E, 134-186 m, 6.1.1980 : 13 ♀ 9.3-12.9 mm (MNHN-Na 5993). — Stn 271, 1°57.8'S, 119°15.0'E, 250 m, 7.11.1980 : 1 ♀ 10.8 mm (MNHN-Na 5980). — Stn 273, 1°56.0'S, 119°16.0'E, 180-220 m, 7.11.1980 : 4 ♀ 11.2-13.7 mm (MNHN-Na 5981).

Non-type material. Indonesia (Makassar Strait). CORINDON 2 : stn 267, 1°56.6'S, 119°16.7'E, 134-186 m, 6.1.1980 : 1 2 12.9 mm (with lateral sinuous ridges of abdominal tergite II continuous).

DESCRIPTION. — Body robust and somewhat dorsoventrally depressed. Integument hard. Eyes kidney shaped. Rostrum about 0.13 (0.11-0.16) carapacial length, with tip cleft or microscopically cleft. Pair of lateral rostral teeth small, but distinct. Carapace about 1.22 (1.12-1.41) times as long as wide; dorsal carina armed with 8-11 teeth; lateral carina I bearing 7-10 teeth; lateral carina II strongly interrupted by hepatic groove, usually bearing two teeth on anterior part and 5-7 teeth and tubercles on posterior part; lateral carina III provided with 8-15 teeth and tubercles. Scaphocerite about 0.28 (0.25-0.34) carapacial length and 1.57 (1.37-1.85) times as long as broad, with outer margin very slightly concave and distolateral tooth generally not nearly reaching distal margin of lamella.

Branchiostegal spine large and wing-like, directed moderately or strongly (in young) outwards and far exceeding distolateral tooth of laterally extended scaphocerite. Pterygostomian spine distinctly larger than antennal spine, on same level with branchiostegal spine and generally failing to reach tip of latter. Pereiopod I exceeding scaphocerite by almost entire subchela. Pereiopod II overreaching scaphocerite by half to entire chela, with carpus almost as long as (0.97-1.02) chela even in spawning females. Pereiopod III long, exceeding scaphocerite by 2/3-1 carpus; pereiopod IV exceeding scaphocerite by 1/2 propodus and dactylus, and pereiopod V by 0-1/2 dactylus. Dactylus of pereiopod V distinctly modified in spawning females; dactylus broadened and somewhat bifurcate, outer end armed with strong, but short, curved spine, enveloped by obtuse flap and long setae, inner end as convex lamellar lobe and slightly twisted. Thoracic sternite VI armed with strongly hooked, but slender, median tooth.

Abdominal sculpturing distinct and subdivided; bearing dorsal carinae on somites II to IV and pair of submedian carinae at somites I, V and VI. Anterior ends of dorsal and submedian carinae of abdominal somites I and II developed into large teeth, while posterior ends of dorsal and submedian carinae on somites IV to VI sharply pointed. Lateral sinuous ridges usually interrupted on abdominal tergite II, but continuous on tergite III. Abdominal somite V usually lacking dorsal spine, but somite VI generally bearing two pairs of dorsolateral spines. Ventral margins of abdominal pleura all acute. Posterodistal tubercle usually present on abdominal pleuron IV and sometimes also on pleuron V. Telson spineless and longer than uropods.

COLORATION. - Not known.

SIZE. - All females, cl 9.3-13.7 mm. Smallest spawning female cl 11.6 mm.

TYPE-LOCALITY. - Makassar, Indonesia.

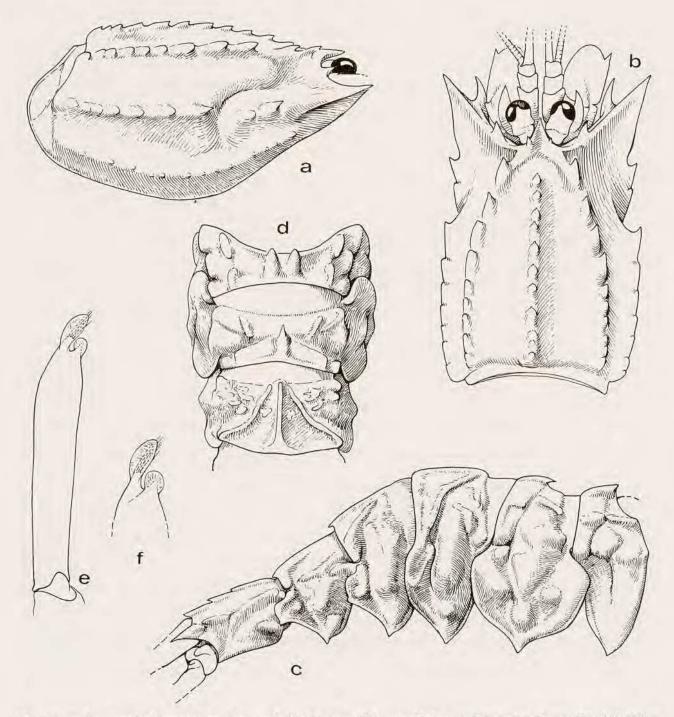


FIG. 14. — Pontocaris laurentae sp. nov. : a-d, ♀ holotype 12.6 mm, Makassar, CORINDON 2, stn 267, 134-186 m (MNHN) : a, lateral view of carapace; b, dorsal view of carapace and anterior appendages; c, lateral view of abdomen; d, dorsal view of abdominal tergites 1-III. — e-f, ♀ (not ovigerous but in spawning molt) paratype 12.8 mm, Makassar, CORINDON 2, stn 267, 134-186 m (MNHN-Na 5993) : e, dactylus of pereiopod V; f, distal end of dactylus of pereiopod V.

DISTRIBUTION. — Only known from the type-locality in Indonesia, at depths of 120-250 m.

REMARKS. — The present species from Indonesia closely resembles *P. major* from the Philippines but differs in the following aspects. The pterygostomian spine is always well below the branchiostegal spine in *P. major*. However, the pterygostomian and branchiostegal spines are more or less at the same level in *P. laurentae*, causing the pterygostomian spine to be covered by the branchiostegal spine when the specimen is viewed laterally. A posterodistal tubercle is usually present on abdominal pleuron IV in *P. laurentae*, but is always absent in *P. major*. Of the 21 *P. laurentae* specimens examined in the present study, only three (14.3%) lack a posterodistal tubercle on one side and two others (9.5%) on both sides of abdominal pleuron IV. *P. laurentae* is considerably smaller in size than *P. major*. The smallest spawning female of *P. laurentae* is cl 11.6 mm as compared to cl 15.2 mm for *P. major*. Moreover, the median tooth of thoracic sternite VI is more slender and curved in *P. laurentae* than in *P. major*. The shape of the dactylus of pereiopod V in spawning females is also different between the two species. The apparently restricted distributions of *P. major* and *P. laurentae*, despite intensive sampling in the Philippines-Indonesia region, further supports the geographical isolation of these two species.

Although no male or ovigerous female of *P. laurentae* was obtained, five out of the 21 females examined are at the spawning molt. The pereiopods II are not particularly lengthened in the spawning females as compared to those of the other females. However, a marked difference is present in the shape of the dactyli of the pereiopods V in these spawning females (slight deviations of the dactylus may also occur in some large, non-spawning females). The ventral margins of the abdominal pleura are less acute in the present species than in *P. major*, but they are always sharper than those of *P. sibogae*. As in *P. major*, only one specimen was found to have a dorsolateral spine on abdominal somite V, otherwise this somite is dorsally unarmed. The armature of abdominal somite V is thus rather useful for separating *P. laurentae* and *P. major* from *P. affinis*, which is sometimes similar in appearance to the former two species.

A female (CORINDON 2, st. 267) identified as the present species has the lateral sinuous ridges on abdominal tergite II continuous, a character thought to be unique in *P. propensalata*. Nevertheless, the anterior and posterior parts of the lateral ridges in this aberrant specimen are of the same width which is rather different from the situation in *P. propensalata*, where the posterior part is generally much wider than the anterior part.

ETYMOLOGY. — This species is named after Mme M. DE SAINT LAURENT for her generous offers of all of her important findings and valuable opinions on these groups of species, as well as for allowing the author to describe this species, even though she had long since noticed that it was undescribed.

### Pontocaris sibogae (de Man, 1918)

Fig. 15

- Aegeon Sibogae de Man, 1918 : 302 (type-locality : Bali Sea, Indonesia); 1920 : 298, pl. 24 figs 72, 72a-f.
- Aegeon Sibogae var. intermedia de Man, 1918 : 303 (type-locality : Strait between Rotti and Timor, Indonesia); 1920 : 300, pl. 24 figs 73, 73a.
- Pontocaris sibogae FUJINO & MIYAKE, 1970 : 301. CHACE, 1984 : 44 (in part).

Pontocaris propensalata - CHACE, 1984 : 43 (in part). Non Bate, 1888.

- Pontocaris pennata HAYASHI, 1986 : 145 (in part). Non Bate, 1888.
- Not Pontocaris sibogae CHACE, 1984 : 44 (in part) (= P. major sp. nov.).

? Aegeon obsoletum - Oshima, 1921 : 123. — Макі & Тsuchiya, 1923 : 74, pl. 6 fig. 7. — Yokoya, 1933 : 43. Non Balss, 1914.

? Pontocaris obsoleta - MIYAKE et al., 1962 : 124. Non Balss, 1914.

? Pontocaris pennata - TORIYAMA & HAYASHI, 1982 : 104. Non Bate, 1888.

MATERIAL EXAMINED. — Indonesia. "Siboga" : stn 15, Bali Sea, south of Kangeang, 7°02.6'S, 115°23.6'E, 100 m, 15.3.1899 : 1  $\Im$  12.0 mm (type, not ovigerous but in spawning molt, ZMA). — Stn 302, strait between Rotti and Timor, 10°27.9'S, 123°28.7'E, 216 m, 2.2.1900 : 1  $\Im$  10.6 mm (type of Aegeon sibogae var. intermedia, not in spawning molt, ZMA).

CORINDON 2 : stn 295, 1°26.5'S, 117°02.1'E, 51-54 m, 11.11.1980 : 1 9 5.3 mm (MNHN-Na 6007).

KARUBAR. Tanimbar Islands : stn CP 65, 9°14'S, 132°27'E, 174-176 m, 1.11.1991 : 2  $\Im$  7.5 and 9.2 mm; 1 ovig.  $\Im$  11.0 mm; 12  $\Im$  7.5-11.2 mm (MNHN). — Stn CP 66, 9°01'S, 132°9'E, 211-217 m, 1.11.1991 : 2  $\Im$  6.7 and 7.4 mm (MNHN).

Philippines. "Albatross" : stn 5241, 6°50'45"N, 126°14'38"E, 393 m, 14.5.1908 : 1 ♂ 10.0 mm; 1 ovig. ♀ 12.5 mm (USNM 205063). — Stn 5242, 6°51'53"N, 126°14'10"E, 349 m, 15.5.1908 : 1 ♂ 8.3 mm, 1 ovig. ♀ 11.0 mm (USNM 205072); 1 ♂ 9.7 mm (USNM 205082).

MUSORSTOM 1 : stn 10, 13°59.8'N, 120°18.2'E, 187-205 m, 19.3.1976 : 1 8 7.8 mm (MNHN-Na 5305). - Stn 18, 13°56.3'N, 120°16.2'E, 150-159 m, 21.3.1976 : 2 9 5.6-7.4 mm (MNHN-Na 5308). - Stn 19, 13°57.8'N, 120°18.2'E, 167-187 m, 21.3.1976 : 4 & 5.8-9.6 mm; 1 ovig. 9 14.5 mm; 5 9 7.2-10.3 mm (MNHN-Na 5300). - Stn 24, 14°00.0'N, 120°18'E, 189-209 m : 3 9 12.6-12.9 mm (MNHN-Na 5285). - Stn 26, 13°59.5'N, 120°16.8'E, 189 m, 22.3.1976 : 2 & 6.5 and 7.8 mm; 3 & 7.8-8.6 mm (MNHN-Na 5286). - Stn 27, 13°59.8'N, 120°15.7'E, 188-192 m, 22.3.1976 : 1 3 6.4 mm; 2 9 9.2 and 10.2 mm (MNHN-Na 5302). - Stn 30, 13°59.7'N, 120°16.7'E, 177-186 m, 22.3.1976 : 1 9 13.1 mm (MNHN-Na 5304). - Stn 31, 14°00.0'N, 120°16'E, 187-195 m, 22.3.1976 : 1 9 10.4 mm (MNHN-Na 5307). — Stn 32, 13°59.4'N, 120°17.7'E, 184-193 m, 23.3.1976 : 1 9 11.8 mm (MNHN-Na 5306). — Stn 34, 13°59.2'N, 120°15.8'E, 188-191 m, 23.3.1976 : 2 ♂ 8.4 and 8.8 mm; 5 ♀ 5.2-14.8 mm (MNHN-Na 5301). -Stn 55, CP4, 13°54.8'N, 120°10.5'E, 194-200 m, 26.3.1976 : 3 9 7.6-9.7 mm (MNHN-Na 5296). - Stn 56, 13°53.1'N, 120°8.9E, 129-134 m, 26.3.1976 : 13 & 6.2-9.4 mm; 2 ovig. 9 12.8 and 13.3 mm; 17 9 4.9-12.6 mm (MNHN-Na 5310). - Stn 62, 13°59.5'N, 120°13.7'E, 179-194 m, 27.3.1976 : 1 & 8.2 mm; 3 & 5.6-9.4 mm (MNHN-Na 5291). -Stn 63, 14°0.5'N, 120°15.8'E, 191-195 m, 27.3.1976 : 1 9 10.9 mm (MNHN-Na 5303). - Stn 64, 13°59.5'N, 120°16.3'E, 194-195 m, 27.3.1976 : 1 9 8.3 mm (MNHN-Na 5297). - Stn 71, 14°9.3'N, 120°26.2'E, 174-204 m, 28.3.1976 : 2 & 7.8 and 8.3 mm; 2 ovig. 9 11.0 and 13.2 mm; 8 9 5.9-12.3 mm (MNHN-Na 5311). - Stn 72, 14°11.8'N, 120°28.7'E, 122-127 m, 28.3.1976 : 11 & 6.9-9.3 mm; 11 & 4.6-7.3 mm (MNHN-Na 5995). - Stn 73, 14°15'N, 120°31.2'E, 70-76 m, 28.3.1976 : 2 & 6.9 and 8.8 mm; 1 & 8.5 mm (MNHN-Na 5295).

MUSORSTOM 2 : stn 1, 14°00.3'N, 120°17.6'E, 188-198 m, 20.11.1980 : 1  $\Im$  8.4 mm (MNHN-Na 5292); 1  $\Im$  10.4 mm (MNHN-Na 8442). — Stn 2, 13°59.9'N, 120°17.1'E, 184-186 m, 20.11.1980 : 1  $\eth$  9.3 mm (MNHN-Na 5293). — Stn 6, 13°56.4'N, 120°20.7'E, 136-152 m, 20.11.1980 : 1  $\circlearrowright$  7.8 mm; 4 ovig.  $\Im$  9.9-13.1 mm (MNHN-Na 5309). — Stn 19, 14°00.5'N, 120°16.5'E, 189 m, 22.11.1980 : 2  $\circlearrowright$  8.2 and 10.0 mm; 1 ovig.  $\Im$  11.6 mm; 1  $\Im$  13.6 mm (MNHN-Na 5298). — Stn 29, 13°42.1'N, 120°49.7'E, 119-204 m, 23.11.1980 : 1 ovig.  $\Im$  9.9 mm; 1  $\Im$  8.2 mm (MNHN). — Stn 35, 13°27.9'N, 121°11.6'E, 160-198 m, 24.11.1980 : 1  $\circlearrowright$  7.2 mm (MNHN-Na 5299). — Stn 51, 13°59.3'N, 120°16.4'E, 170-187 m, 27.11.1980 : 1  $\circlearrowright$  9.6 mm (MNHN-Na 10690). — Stn 52, 13°59.1'N, 120°18.7'E, 181-190 m, 27.11.1980 : 1  $\circlearrowright$  13.1 mm (MNHN-Na 5290). — Stn 59, 14°0.3'N, 120°16.5'E, 186-190 m, 28.11.1980 : 1  $\textdegree$  8.9 mm (MNHN-Na 5294). — Stn 63, 14°7.2'N, 120°15'E, 215-230 m, 29.11.1980 : 1  $\circlearrowright$  11.4 mm (MNHN-Na 8443). — Stn 67, 14°0.1'N, 120°18.5'E, 193-199 m, 29.11.1980 : 1  $\circlearrowright$  10.2 mm (MNHN-Na 5287). — Stn 72, 14°0.1'N, 120°17.8'E, 182-197 m, 30.11.1980 : 1  $\circlearrowright$  10.1 mm; 1  $\textdegree$  10.8 mm (MNHN-Na 5288).

MUSORSTOM 3 : stn 86, 14°00.4'N, 120°17.8'E, 187-192 m, 31.5.1985 : 1  $\Im$  11.8 mm (MNHN). — Stn 87, 14°00.6'N, 120°19.6'E, 191-197 m, 31.5.1985 : 2  $\Im$  7.5 and 8.0 mm; 3  $\Im$  8.5-13.4 mm (MNHN). — Stn 88, 14°00.5'N, 120°17.4'E, 168-173 m, 31.5.1985 : 4  $\Im$  7.8-9.1 mm; 1 ovig.  $\Im$  12.7 mm; 10  $\Im$  7.0-11.5 mm (MNHN). — Stn 90, 14°00.1'N, 120°18.6'E, 195 m, 31.5.1985 : 4  $\Im$  8.9-12.6 mm (MNHN). — Stn 91, 14°00.1'N, 120°17.8'E, 190-203 m, 31.3.1985 : 1  $\Im$  9.5 mm (MNHN). — Stn 96, 14°00.3'N, 120°17.3'E, 190-194 m, 1.6.1985 : 3  $\Im$  8.5-9.0 mm; 4  $\Im$  7.3-12.2 mm (MNHN). — Stn 98, 14°00.2'N, 120°17.9'E, 194-205 m, 1.6.1985 : 2  $\Im$  9.9 and 11.6 mm (MNHN). — Stn 100, 14°00.0'N, 120°17.6'E, 189-199 m, 1.6.1985 : 7  $\Im$  8.1-9.8 mm; 17  $\Im$  6.9-12.3 mm (MNHN). — Stn 101, 14°00.1'N, 120°17.6'E, 189-199 m, 1.6.1985 : 7  $\Im$  8.1-9.8 mm; 17  $\Im$  6.9-12.3 mm (MNHN). — Stn 101, 14°00.1'N, 120°17.6'E, 189-199 m, 1.6.1985 : 7  $\Im$  8.1-9.8 mm; 17  $\Im$  6.9-12.3 mm (MNHN). — Stn 101, 14°00.1'N, 120°17.6'E, 189-199 m, 1.6.1985 : 7  $\Im$  8.1-9.8 mm; 17  $\Im$  6.9-12.3 mm (MNHN). — Stn 101, 14°00.1'N, 120°17.6'E, 189-199 m, 1.6.1985 : 2  $\Im$  7.0 and 8.3 mm; 7  $\Im$  8.3-11.9 mm (MNHN). — Stn 103, 14°00.4'N, 120°18.1'E, 193-200 m, 1.6.1985 : 2  $\Im$  9.8 and 12.7 mm (MNHN). — Stn 108, 14°01.1'N, 120°17.9'E, 188-195 m, 2.6.1985 : 3  $\Im$  6.9-8.7 mm; 4  $\Im$  8.0-11.4 mm (MNHN). — Stn 109, 14°00.2'N, 120°17.6'E, 190-198 m, 2.6.1985 : 1  $\Im$  7.8-9.0 mm; 7  $\Im$  8.1-11.4 mm (MNHN). — Stn 111, 14°00.1'N, 120°17.5'E, 193-205 m, 2.6.1985 : 4  $\Im$  7.8-9.0 mm; 7  $\Im$  8.1-11.4 mm (MNHN). — Stn 112, 14°00.2'N, 120°19.2'E, 187-199 m, 2.6.1985 : 1  $\Im$  10.36 mm (MNHN). — Stn 116, 12°32.2'N, 120°46.4'E, 804-812 m, 3.6.1985 : 1  $\Im$  10.3 mm (MNHN).

**New Caledonia**. BIOCAL : stn CP 105, 21°30.71'S, 166°21.72'E, 330-335 m, 8.9.1985 : 1 ♀ 11.1 mm (MNHN). — Stn CP 110, 22°12.38'S, 167°6.43'E, 275-320 m, 9.9.1985 : 2 ♀ 7.9 and 8.0 mm (MNHN).

MUSORSTOM 4 : stn DW 162, 18°35'S, 163°10.3'E, 535 m, 16.9.1985 : 1 & 8.86 mm (MNHN).

LAGON : stn 835, 20°46.8'S, 165°17.3'E, 135-150 m, 11.1.1987 : 1 9 7.2 mm (MNHN).

HALIPRO 1 : stn 851, 21°43.960'S, 166°37.429'E, 314-364 m, 19.3.1994 : 1 ♀ 12.1 mm (MNHN). — Stn 866, 21°26.910'S, 166°17.229'E, 550-600 m, 22.3.1994 : 1 ovig. ♀ 12.0 mm (MNHN).

Loyalty Islands. MUSORSTOM 6 : stn CP 455, 21°0.65'S, 167°26.08'E, 260 m, 20.2.1989 : 1 3 9.4 mm (MNHN).

Taiwan. Tong-Kong, Ping-Tong County, south-western Taiwan, fish market, commercial trawlers, about 150 m, 31.10.1984 : 1 ovig. ♀ 13.6 mm; 5 ♀ 11.2-13.7 mm (MNHN, NTOU in exchange). — 2.12.1984 : 1 ♂ 9.2 mm (NTOU);

2 9 13.1 and 13.7 mm (MNHN, NTOU in exchange). — 29.10.1988 : 1 ovig. 9 13.3 mm (MNHN, NTOU in exchange).

- 3.3.1989 : 2 9 12.0 and 13.4 mm (MNHN, NTOU in exchange). - 26.1.1994 : 3 ovig. 9 12.2-15.3 mm (NTOU).

Shin-Ta-Kong, Kaio-Shung County, south-western Taiwan, fish market, commercial trawlers, about 100 m, 6.5.1988 : 1 ovig. ♀ 12.7 mm; 1 ♀ 11.8 mm (NTOU).

Japan. Tosa Bay, 100-115 m, 30.8.1982 : 2 ♂ 10.4 and 10.8 mm; 1 ♀ 11.0 mm (as "P. pennata" in HAYASHI, 1986, SUF).

DIAGNOSIS. — Tip of rostrum varying from entire (less often) to microscopically cleft (most often) or cleft. Carapace about 1.15 (1.11-1.2) times as long as wide; dorsal carina armed with 7-11 (mostly 10) teeth; lateral carina I bearing 7-10 teeth; lateral carina II having two teeth on anterior part and 5-8 teeth on posterior part; lateral carina III usually with 9-17 teeth and tubercles. Scaphocerite about 1.36 (1.25-1.65) times as long as broad. Branchiostegal spine large and wing-like, directed moderately or sometimes strongly outwards, generally almost reaching (in males) or just exceeding (in females) tip of distolateral tooth of laterally extended scaphocerite. Pterygostomian spine larger than antennal spine and generally nearly reaching tip of branchiostegal spine, below or almost on same level with latter spine. Pereiopod II considerably lengthened in spawning females and with carpus about 1.63 (1.45-1.89) times longer than chela, but dactylus of pereiopod V remaining simple. Thoracic sternite VI armed with large, hooked, median tooth. Abdominal sculpturing distinct and subdivided; lateral sinuous ridges on abdominal tergite II and, usually, at least one side of tergite III interrupted dorsally. Abdominal somite IV bearing strong posteromedian spine. Generally two pairs (2-8) of dorsolateral spines present on abdominal

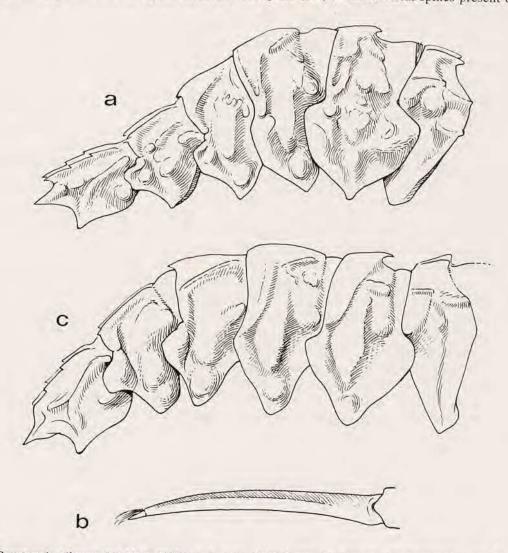


FIG. 15. — Pontocaris sibogae (de Man, 1918) : a-b, ovig. ♀ 13.3 mm, Philippines, MUSORSTOM 1, stn 56, 129-134 m (MNHN-Na 5310) : a, lateral view of abdomen; b, dactylus of pereiopod V. — c, ♂ 9.2 mm, Philippines, MUSORSTOM 1, stn 56, 129-134 m (MNHN-Na 5310) : lateral view of abdomen.

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somite VI, but none on somite V. Ventral margins of abdominal pleura generally subacute in females, but bluntly angular and occasionally even slightly truncate in males. Posterodistal tubercle usually present on both abdominal pleura IV and V. Eggs numerous and subspherical, about 0.4-0.5 mm in diameter.

COLORATION. — Body molted with orange and brown, covered with broad, pale, transverse bands on branchiostegal spines and mid-carapace. Eyes brownish. Antennal flagella same colour as body. Tip of branchiostegal spine red-brown. Distal margin of propodus of pereiopod I white. Ventral margins of abdominal pleura, pleopods, and sometimes also ventral carapace, pink. Tail fan somewhat whitish, with outer border of exopod of uropod and tip of telson brownish. Eggs orange.

SIZE. — Largest female cl 15.3 mm and largest male cl 10.8 mm. Smallest spawning female cl 9.9 mm.

DISTRIBUTION. — Along the western periphery of the Pacific Ocean from Japan to the East China Sea, Taiwan, Philippines, Indonesia, Loyalty Islands and New Caledonia. At depths of 70-812 m, but mostly less than 335 m.

REMARKS. — P. sibogae appears to be very common in the Philippines where it is the dominant species of the genus. Nevertheless, there are large variations in the morphological characters of this species. Without the discovery that the pereiopod modification in spawning females of P. sibogae is completely different from that in most of the other species of the genus, most of the material in the present study would probably have been misidentified, as in previous works.

Of the 279 specimens examined, 234 (83.9%) have posterodistal tubercles present on abdominal pleuron IV, including 53 (19.0%) in which only one side of the pleuron bears a tubercle. There is generally no dorsal spine on abdominal somite V. However, in 26 specimens (9.3%) identifiable as the present species, a dorsolateral spine is present on abdominal somite V and in 11 others (3.9%) there is a pair of dorsolateral spines. As for the lateral sinuous ridges on abdominal tergite III, 31 specimens (11.1%) have the ridges on one side not interrupted and in 11 others (3.9%) the ridges are continuous on both sides. Nevertheless, 8 (all females, including the type of Aegeon sibogae var. intermedia, cl 8.7-13.6 mm; two ovigerous and two at the spawning molt) of these 11 specimens have the carpi of the pereiopods II 1.4 to 1.7 times longer than the chelae and the dactyli of the pereiopods V simple. The remaining three specimens (one male cl 7.0 mm and two young females cl 6.6-8.5 mm) have the ventral margins of the abdominal pleura bluntly angular and both sides of pleuron IV bearing posterodistal tubercles. They are, therefore, readily distinguishable from P. major and P. laurentae. However, one of these aberrant specimen from the Philippines shows close resemblances to P. affinis affinis. Besides the lateral ridges on abdominal tergite III being continuous on both sides, a pair of dorsolateral spines is present on abdominal somite V in this spawning female (cl 12.7 mm; without eggs). Nevertheless, its rostrum is entire, the 14 or more tubercles on lateral carapacial carina III are large and distinct, and the median tooth on thoracic sternite VI is very large and hooked. Furthermore, the ventral margins of its abdominal pleura are not acute and the lateral sinuous ridges on abdominal tergite III converge toward the anterior end of the median carina (i.e. as in most of the P. sibogae material). In all but one small female of P. affinis affinis the lateral sinuous ridges on abdominal tergite III converge at a distance behind the anterior end of the median carina. Since P. affinis has not been found outside the Indian Ocean and only one such intermediate specimen is known from the Philippines, despite the extensive sampling in this area, it is believed that the intermediate characteristics of this female are merely representative of the large variations exhibited in P. sibogae.

The materials from the different localities are very similar and all display large variations in the morphological characters. The type from Indonesia is a spawning female and still has intact pereiopods II and V. Its characteristics are all "typical" of the species (i.e. with carpus of the pereiopod II 1.6 times longer than chela; see also DE MAN. 1920, figs 72, 72a, 72f). The type of *Aegeon sibogae* var. *intermedia* is a non-spawning female and its characters conform well with the typical form, except for the lateral sinuous ridges on abdominal somite III being continuous (discussed further in "Remarks" under *P. major*). The differences in the thoracic sternites and the length of the carpus of the pereiopod II, mentioned by DE MAN (1920) between the variety *intermedia* and *P. sibogae*, are now known to be only part of the peculiar polymorphisms displayed by the females of this genus. By considering the

large variations exhibited in the abundant material available for the present study, it can be readily determined that the type of *Aegeon sibogae* var. *intermedia* is truly a "variation" of the typical form, as concluded by FUJINO and MIYAKE (1970) and CHACE (1984), though these authors based their conclusions on very different reasons from those noted in the present study.

Although the tubercles on lateral carapacial carina III are usually well-developed in the present species, they may be barely distinguishable in certain small males. As in many other species of the genus, the branchiostegal spine is generally larger and directed more outwards in the southern populations (i.e. those from New Caledonia and adjacent areas), but slightly shorter and projecting less outwards in the northern populations (i.e. those from Taiwan). Not only do all of the 54 spawning females (21 ovigerous) have the carpi of their pereiopods II distinctly lengthened and extending beyond midlength of the subchelae of pereiopods I, but the same carpi of large non-spawning females are often variably lengthened. The interlocking between the thoracic sternum and the ventral carapace appears to be most developed in *P. sibogae*, as the thoracic sternite V is also more or less interlocked with the carapace even in juvenile specimens of this species.

# Pontocaris pennata Bate, 1888

### Figs 16-17

Pontocaris pennata Bate, 1888 : 499 (in part), pl. 91 (type-locality : Arafura Sea). — ORTMANN, 1895 : 175. — HOLTHUIS, 1980 : 152 (in part). — MIYAKE, 1982 : 68, pl. 23 fig. 4. — CHACE, 1984 : 43. — HAYASHI, 1986 : 145 (in part), pl. 96.

Aegeon obsoletum Balss, 1914a : 70, pl. 1 fig. 3 (type-locality : Japan); 1924 : 51.

Not Pontocaris pennata Bate, 1888 : 499 (male only) [= P. arafurae (Bruce, 1888)].

Not Aegeon pennata - BALSS, 1914b : 137 (?in part); 1915 : 32 (? in part) (= P. profundior sp. nov.).

Not Aegeon pennata - BALSS, 1914b : 137 (?in part); 1915 : 32 (? in part). — KEMP, 1916 : 376 (? in part, those from the Arabian Sea and the Persian Gulf) (= P. affinis allodactylus subsp. nov.).

Not Aegeon pennata - DE MAN, 1920 : 294, pl. 24 figs 70, 70a-d (= P. spinifera sp. nov.).

Not Pontocaris pennata - HOLTHUIS, 1980 : 152 (in part) [= P. affinis affinis (Alcock, 1901), P. affinis allodactylus subsp. nov., P. spinifera sp. nov.].

Not Pontocaris pennata - HAYASHI, 1986 : 145 (in part) [= P. sibogae (de Man, 1918)].

? Aegeon obsoletum - Oshima, 1921 : 123. — МАКІ & ТSUCHIYA, 1923 : 74, pl. 6 fig. 7. — YOKOYA, 1933 : 43 [or = P. sibogae (de Man, 1918)].

? Pontocaris obsoleta - MIYAKE et al., 1962 : 124 [? or P. sibogae (de Man, 1918)].

?Pontocaris pennata - TORIYAMA & HAYASHI, 1982 : 104 [? or P. sibogae (de Man, 1918)].

? Not Aegeon pennata - KEMP, 1916 : 376 (in part, those from India) [= P. affinis affinis (Alcock, 1901)].

? Not Pontocaris pennata - SANKOLLI & SHENOY, 1979 : 62 [= P. affinis affinis (Alcock, 1901)]

? Not Pontocaris pennata - LALITHA DEVI, 1986 : 171, fig. 4 (= P. propensalata Bate, 1888).

MATERIAL EXAMINED. — Indonesia. "Challenger", stn 190, Arafura Sea, 8°56'S, 136°5'E, 90 m, 12.9.1874 : 1 ♀ 7.2 mm (lectotype); 1 ♀ 6.7 mm (paralectotype, NHM).

CORINDON 2 (Makassar Strait) : stn 201, 1°10.2'S, 117°06.1'E, 21 m, 30.10.1980 : 1 ovig. ♀ 7.5 mm (MNHN-Na 5996). — Stn 205, 1°07.8'S, 117°18.7'E, 49 m, 30.10.1980 : 3 ♂ 5.9-6.2 mm; 1 ovig. ♀ 8.6 mm; 1 ♀ 6.2 mm (MNHN-Na 5997).

**Philippines**. "Albatross" : stn 5376, 13°42'50"N, 121°51'30"E, 165 m, 2.3.1909 : 1  $\bigcirc$  9.9 mm (USNM 205043). — Stn 5432, 10°37'50"N, 120°12'E, 93 m, 8.4.1909 : 1 ovig.  $\heartsuit$  10.0 mm (USNM 205038). — Stn 5442, 16°30'36"N, 120°11'06"E, 82 m, 11.5.1909 : 1 ovig.  $\heartsuit$  9.8 mm (USNM 205042). — Stn 5477, 10°44'45"N, 125°12'30"E, 88 m, 29.7.1909 : 1  $\heartsuit$  8.1 mm (USNM 205039). — Stn 5480, 10°44'36"N, 125°19'E, 113 m, 29.7.1909 : 1  $\heartsuit$  7.2 mm (USNM 205036).

MUSORSTOM 1 : stn 45, 13°45.5′N, 120°23.5′E, 100-180 m, 24.3.1976 : 1 ♀ 6.6 mm (MNHN-Na 5289). — Stn 73, 14°15.0′N, 120°31.2′E, 70-76 m, 28.3.1974 : 5 ♂ 6.1-7.3 mm; 4 ovig. ♀ 8.5-9.6 mm; 5 ♀ 5.5-9.0 mm (MNHN-Na 5998).

South China Sea. "Albatross" : stn 5302, 21°42'N, 114°50'E, 70 m, 9.8.1908 : 1 ♂ 6.6 mm; 1 ovig. ♀ 11.4 mm; 1 juvenile 4.6 mm (USNM 205041). — Stn 5309, 21°53'N, 115°51'E, 113 m, 4.11.1908 : 1 ovig. ♀ 8.6 mm; 1 ♀ 10 mm (USNM 205040).

**Taiwan**. Tong-Kong, Ping-Tong County, south-western Taiwan, fish market, commercial trawlers, about 150 m, 29.12.1984 : 1 ovig. ♀ 10.9 mm (NTOU). — 31.10.1988 : 1 ♀ 8.5 mm (MNHN, NTOU in exchange).

### T.-Y. CHAN

Japan. Sagami Bay, 150 m : 1 & 7.6 mm; 1 & 10.8 mm (syntypes of Aegeon obsoletum, ZSM 430/1).

Off Enoshima, 80 m, 12.6.1904 : 1 ovig. 9 11.5 mm; 1 9 12.2 mm, DOFLEIN coll., Nr. 2683 (syntypes of Aegeon obsoletum, ZSM 430/3).

Dzushi, 50-100 m, 12.11.1904 : 1 ♂ 6.5 mm; 1 ovig. ♀ 10.5 mm, DOFLEIN coll., Nr. 2684 (syntypes of Aegeon obsoletum, ZSM 430/2).

Toshi Bay, 80 m, 3.3.1981 : 2 9 11.9 and 12.5 mm (specimens in HAYASHI, 1986, SUF). — *Ibidem*, 75 m, 18.5.1987 : 1 & 7.0 mm; 1 ovig. 9 9.9 mm (SUF).

DIAGNOSIS. — Tip of rostrum microscopically cleft or cleft (most). Carapace about 1.09-1.29 times as long as wide; dorsal carina armed with 8-10 teeth; lateral carina I bearing 8-10 teeth; lateral carina II usually bearing two teeth on anterior part and 2-7 teeth and tubercles on posterior part; lateral carina III provided with 1-10 teeth and tubercles. Scaphocerite about 1.43-1.52 times as long as broad. Branchiostegal spine large, directed from moderately outwards to nearly straight (more often in large females), reaching 4/5 or just exceeding outer margin of laterally extended scaphocerite. Pterygostomian spine more or less as large as antennal spine but reaching far behind branchiostegal spine, below or at same level as latter. Pereiopod II with carpus about as long as (0.9-1.12) chela, even in spawning females. Dactylus of pereiopod V strongly modified in spawning females: dactylus paddle-shaped and twisted, distal end convex and lamellar, outer end armed with long strong curved spine enveloped by longer flap and setae. Thoracic sternite VI not carinate medially. Abdominal sculpturing distinct and subdivided; lateral sinuous ridges interrupted on both tergites II and III. Abdominal somite IV bearing a strong posteromedian spine. Usually one pair of dorsolateral spines present on abdominal somite V and three pairs (sometimes two or four pairs) on somite VI. Ventral margins of abdominal pleura generally pointed, except sometimes somewhat truncate on posterior pleura in small males. Posterodistal tubercle absent on abdominal pleuron IV, but usually present on pleuron V. Eggs numerous and subspherical, 0.45-0.55 mm in diameter.

COLORATION. — Body reddish, sometimes with narrow, transverse, pale band at mid-carapace. Antennal flagella same colour as body, but pereiopods paler. Eyes deep-brown. Ventral parts of abdominal pleura whitish. Tail fan covered with transverse white band at middle. Eggs orange.

SIZE. - Largest female cl 12.5 mm and largest male cl 7.6 mm. Smallest spawning female cl 8.6 mm.

DISTRIBUTION. — Along the western side of the Pacific, known with certainty from Japan, Taiwan, the South China Sea, the Philippines and Indonesia. At depths of 17-165 m.

REMARKS. — The type series of *P. pennata* from the "Challenger" expedition consists of two young females (the larger female has the mouthparts dissected) and one male. As already mentioned by BATE (1888) and CALMAN (in KEMP, 1916), the tip of the rostrum is cleft in the females but entire in the male. The branchiostegal spine is directed strongly outward in the larger female, moderately outward in the smaller female and is almost straight in the male. The lateral sinuous ridges on abdominal tergite III are interrupted in the females, but continuous in the male. Moreover, both females bear a strong posteromedian spine on abdominal somite IV, whilst this spine is absent in the male. Although all have the posterior parts of the lateral carapacial carinae II bearing fewer than four teeth, the anterior part of this carina has two teeth in the larger female, but only one tooth in the smaller female and male. It is obvious that more than one species is represented in the type series of *P. pennata*. Since BATE's (1888) descriptions and figures were mainly based on the larger female, it is here chosen as the lectotype. The male is now known to belong to *Pontocheras arafurae* described by BRUCE (1988). The smaller female, although having only one tooth on the anterior part of the lateral carapacial carina II, is generally much more similar to the lectotype than to the male.

The material from Taiwan, the Philippines, the South China Sea and Makassar are almost identical, except that the length of the outer spine at the dactylus of the pereiopod V in spawning females is rather variable, perhaps caused by damages. The abdominal sculpturing is very deep and the spines on the body are rather large in the type series but these may due to an artifact of preservation. Since the shape of the branchiostegal spine in the species of this genus is often variable and tends to be directed more outward in the southern populations, it is highly likely that the strongly outwardly directed branchiostegal spine in the lectotype is atypical. On the other hand, some

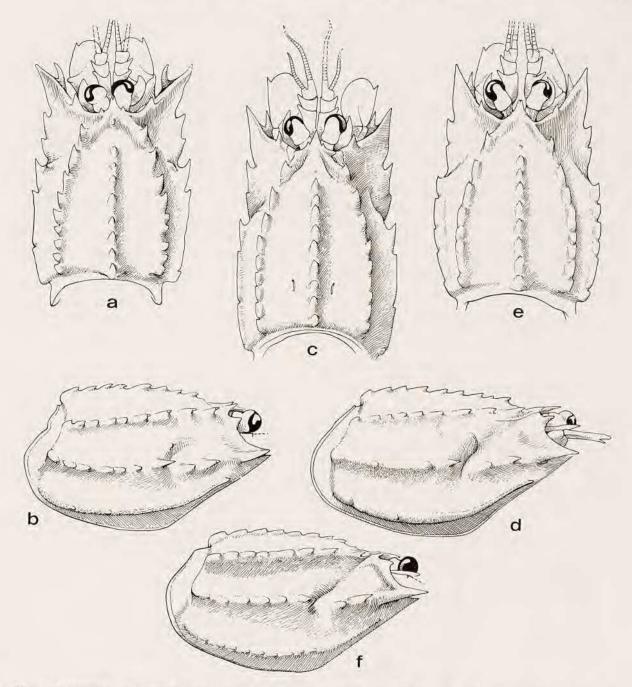


FIG. 16. — Pontocaris pennata Bate, 1888 : a-b, ♀ lectotype 7.2 mm, Arafura Sea, "Challenger", stn 190, 90 m (BMNH) : a, dorsal view of carapace and anterior appendages; b, lateral view of carapace. — c-d, ovig. ♀ 9.4 mm, Philippines, MUSORSTOM 1, stn 73, 70-76 m (MNHN-Na 5998) : c, dorsal view of carapace and anterior appendages; d, lateral view of carapace. — e-f, ovig. ♀ 11.5 mm (syntype of Aegeon obsoletum Balss, 1914), Japan, Bei Enoshima, 80 m (ZSM 430/3) : e, dorsal view of carapace and anterior appendages; f, lateral view of carapace.

young specimens from the Philippines and Makassar have the branchiostegal spines very similar to those of the smaller of the female syntypes; four specimens also have the anterior part of the lateral carapacial carina II bearing a single tooth on only one side. As in the other species that have the dactyli of pereiopods V distinctly modified in spawning females, some large non-spawning females of this species have their dactyli slightly modified.

The lateral carapacial carina III of the present species has always been described as smooth or entire by previous authors (KEMP, 1916; DE MAN, 1920; CHACE, 1984). However, a few tubercles may sometimes be present on this carina. Furthermore, the number of tubercles on the lateral carapacial carinae II and III is generally higher in Japanese material. There are 4-7 tubercles on the posterior part of the lateral carapacial carina II in Japanese specimens while only 2-6 tubercles are present in those from southern localities. On the lateral carapacial carina III, the Japanese material has 1-10 (mostly 4-8) tubercles, but the other specimens have 1-6 tubercles. The size of the Japanese material also appears to be slightly larger. Nevertheless, specimens from the different localities all lack a median carina on thoracic sternite VI, and the shape of the dactylus of pereiopod V in spawning females is almost identical. Therefore, it seems unnecessary to revive the name *obsoletum* for the Japanese population.

Only *P. pennata*, *P. sibogae* and *P. spinifera* of this genus have the lateral sinuous ridges on abdominal tergite III dorsally interrupted. Furthermore, as suggested by BATE (1888), the absence of a median carina on thoracic sternite VI separates-*P. pennata* from most other species of the genus. Although *P. pennata* can also be distinguished from *P. sibogae* by the completely different modification of the pereiopods in spawning females, most of the records of the present species from Japan and Taiwan (OSHIMA, 1921; MAKI & TSUCHIYA, 1923; YOKOYA, 1933; MIYAKE *et al.*, 1962; TORIYAMA & HAYASHI, 1982) are too brief to determine whether they refers truly to *P. pennata* or represent *P. sibogae*.

*P. pennata* appears to be restricted to the western periphery of the Pacific Ocean, being less widely distributed in the Indo-West Pacific than previously thought. The records of *P. pennata* from the Red Sea (BALSS, 1914b, 1915) and the Indian Ocean (KEMP, 1916; SANKOLLI & SHENOY, 1979; LALITHA DEVI, 1986) need to be verified.

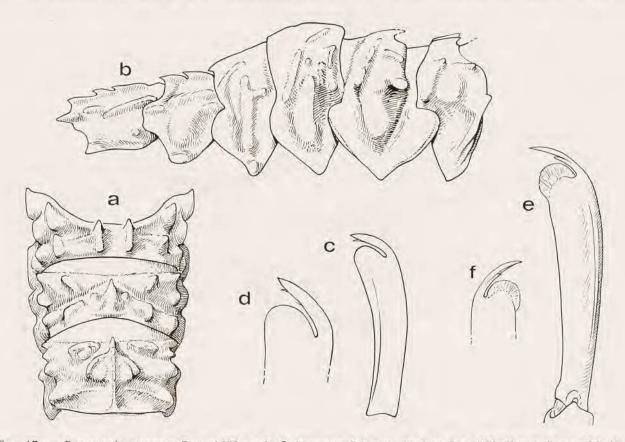


FIG. 17. — Pontocaris pennata Bate, 1888 : a-b, ♀ lectotype 7.2 mm, Arafura Sea, "Challenger", stn 190, 90 m (BMNH) : a, dorsal view of abdominal tergites I-III; b, lateral view of abdomen. — c-d, ovig. ♀ 11.5 mm (syntype of Aegeon obsoletum Balss, 1914), Japan, Bei Enoshima, 80 m (ZSM 430/3) : c, dactylus of pereiopod V; d, distal end of dactylus of pereiopod V. — e-f, ovig. ♀ 9.4 mm, Philippines, MUSORSTOM 1, stn 73, 70-76 m (MNHN-Na 5998) : e, dactylus of pereiopod V; f, distal end of dactylus of pereiopod V.

# Pontocaris spinifera sp. nov.

## Fig. 18

Aegeon pennata - DE MAN, 1920 : 294, pl. 24 figs 70, 70a-d. Non Bate, 1888. Pontocaris pennata - HOLTHUIS. 1980 : 152 (in part). Non Bate, 1888.

MATERIAL EXAMINED. — Holotype. Indonesia. "Siboga" : stn 312, Saleh Bay, Sumbawa, Flora Sea, 8°19'S, 117°41'E, 274 m, 14.2.1900 :  $1 \$  10.5 mm (not ovigerous, but in spawning molt, ZMA).

**Paratypes.** Indonesia. "Siboga" : stn 306, Lobetobi Strait, 8°27'S, 122°54.5'E, 247 m, 8.2.1900 : 2 ♂ 8.9 and 9.8 mm; 1 ovig. ♀ 11.6 mm; 1 ♀ 11.3 mm (ZMA). — Stn 312, Saleh Bay, Sumbawa, Flora Sea, 8°19'S, 117°41'E, 274 m, 14.2.1900 : 2 ♂ 8.8 and 10.7 mm (ZMA).

DESCRIPTION. — Body robust and somewhat dorsoventrally depressed. Integument hard. Eyes kidney-shaped. Rostrum about 0.13 (0.1-0.15) carapacial length, tip always cleft. Paired lateral rostral teeth small but distinct. Carapace 1.23-1.38 times as long as wide; dorsal carina armed with 8-9 teeth; lateral carina I bearing 8-10 teeth; lateral carina II strongly interrupted by hepatic groove, bearing two teeth on anterior part and 2-5 teeth on posterior part; lateral carina III provided with 1-2 teeth or tubercles. Scaphocerite about 0.21 (0.19-0.23) carapacial length and 1.22 (1.09-1.32) times as long as broad; outer margin straight and distolateral tooth not quite reaching distal margin of lamella.

Branchiostegal spine very large and directed strongly outwards, far exceeding distolateral tooth of laterally extended scaphocerite. Pterygostomian spine more or less as large as antennal spine, generally below and not

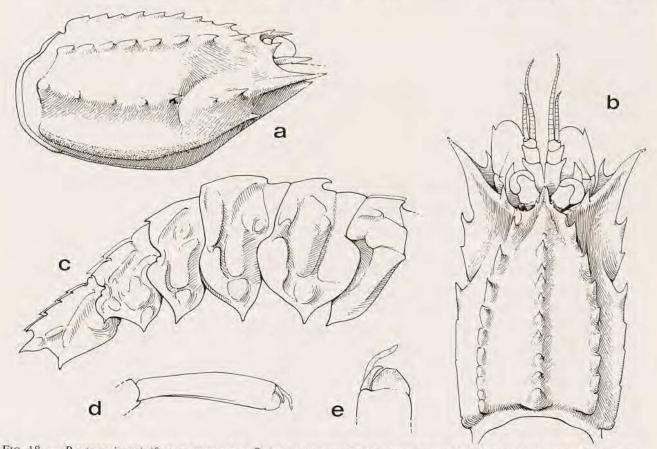


FIG. 18. — Pontocaris spinifera sp. nov. : a-e, ♀ (not ovigerous but in spawning molt) holotype 10.5 mm (ZMA), Flora Sea, "Siboga", stn 312, 274 m : a, lateral view of carapace and anterior appendages; b, dorsal view of carapace and anterior appendages; c, lateral view of abdomen; d, dactylus of pereiopod V; e, distal end of dactylus of pereiopod V.

nearly reaching as far as behind branchiostegal spine. Pereiopods I exceeding scaphocerite by entire subchela. Pereiopod II overreaching scaphocerite by about half chela, with carpus only slightly longer (1.03-1.2) than chela even in spawning females. Pereiopod III long and exceeding scaphocerite by 1/3-3/4 carpus; pereiopod IV by 1/3 propodus to dactylus. Pereiopod V failing to, or just reaching distal margin of scaphocerite, with dactylus strongly modified in spawning females : dactylus paddle-shaped and twisted, distal end convex and lamellate, outer end armed with a strong curved spine, enveloped by longer flap and setae. Thoracic sternite VI not carinate medially.

Abdomen with sculpturing distinct and subdivided; bearing dorsal carinae on somites II to IV and pair of submedian carinae on somites I, V and VI. Dorsal and submedian carinae at abdominal somites I and II anteriorly developed into teeth, while posterior ends of dorsal and submedian carinae of IV to VI are sharply pointed. Lateral sinuous ridges interrupted on abdominal tergites II and III. One pair of dorsolateral spines usually present on abdominal somite V and 2-4 (mostly 2-3) pairs on somite VI. Ventral margins of all abdominal pleura elongate and acute. Abdominal pleuron IV usually lacking posterodistal tubercle, but a strong posterodistal spine is always present on pleuron V. Eggs numerous and subspherical, about 0.5 mm in diameter.

COLORATION. - Not known.

SIZE. - Largest female cl 11.6 mm and largest male cl 10.7. Smallest spawning female cl 10.5 mm.

TYPE-LOCALITY. - Flores Sea, Indonesia.

DISTRIBUTION. - Only known from Indonesia, at depths of 247-274 m.

REMARKS. — A detailed descriptions of this species has also been given by DE MAN (1920) under the name "Aegeon pennata". Indeed, P. spinifera closely resembles P. pennata and lacks a median carina on thoracic sternite VI. Nevertheless, the branchiostegal spines of the "Siboga" specimens are always larger and directed more outwards than those identified as P. pennata in the present study (including the lectotype female). The sharply-pointed abdominal pleura of the present form are much more elongate and acute than those of P. pennata and comparable to those of P. laurentae. More importantly, the abdominal pleuron V of the "Siboga" material is always armed with a strong posterodistal spine, which is generally wanting in the other species of the genus except P. profundior (though a posterodistal tubercle may be present in some species). It is worth noting that the posterodistal tubercle on abdominal pleuron V in three P. pennata specimens is rather sharp. However, it is not as elongate and spine like as in DE MAN's (1920) specimens. Thus, it seems appropriate to treat the present form as a distinct species.

ETYMOLOGY. — The Latin *spinifera* refers to the bearing of an additional spine on abdominal pleuron V in the present form as compared to the closely related species *P. pennata*.

# Genus PARAPONTOCARIS Alcock, 1901

Parapontocaris Alcock, 1901: 120 (Gender : feminine; type-species : Crangon bengalensis Wood-Mason & Alcock, 1891). — CHACE, 1984: 29. — CHRISTOFFERSEN, 1990: 99. — HOLTHUIS, 1993: 294.

DIAGNOSIS. — Body rather large but slender. Rostrum short and pointed, with two pairs of lateral teeth. Carapace 1.33-2.07 times as long as broad, having 4-5 dorsal teeth; lateral carina I bearing 4-5 (very rarely 3 or 6) teeth, with anteriormost tooth distinctly separated from others; lateral carina II having 3-8 teeth, continuous with antennal spine; lateral carina III bearing 1-9 teeth, continuous with branchiostegal spine. Hepatic groove absent. Branchiostegal spine not particularly large, extending over less than basal 1/7 of outer margin of laterally extended scaphocerite. Pterygostomian spine distinctly smaller than antennal spine. Scaphocerite narrow, 1.81-2.3 times as long as wide; with distolateral tooth overreaching distal margin of lamella and considerably larger than antennal spine. Thoracic sternum not interlocked with ventral carapace. A pair of ventral teeth present behind coxae of pereiopods V in males and non-spawning females. Pereiopods not modified in spawning females. Abdominal sculpturing rather simple, mainly composed of straight carinae and ridges. Abdominal sternites without median spine. Abdominal pleura varying from slightly triangular in males to somewhat quadrangular in ovigerous females. Telson armed with two pairs of dorsolateral and three pairs (outer pair very short) of terminal spines.

DISTRIBUTION. - Indo-West Pacific and Caribbean Sea. At depths of 215-885 m.

REMARKS. — Parapontocaris was originally proposed by ALCOCK (1901) as a subgenus of Aegaeon ("Aegeon" in ALCOCK, 1901) and contained only two species at that time. KEMP (1916) and DE MAN (1920) argued that such a subdivision was not necessary, as some species were intermediate between Aegaeon (s. st.) and those referred to Parapontocaris by ALCOCK (1901). With the subsequent findings of four more species closely resembling ALCOCK's (1901) original species, CHACE (1984) decided to revive Parapontocaris as a full genus, emphasizing the form of the rostrum and the unarmed abdominal sternites.

KEMP (1916) and DE MAN (1920) based their concept of Aegaeon on the P. propensalata group, instead of the type-species, A. cataphractus. With the discovery of the peculiar interlocking mechanism between the thoracic sternum and the ventral carapace, as well as the ability to modify the pereiopods in the members of the P. propensalata group, these species no doubt require a genus of their own. The remaining species consist of 6 rather homogenous species (i.e. those referred to Parapontocaris by CHACE, 1984) and five other, highly heterogeneous species. Since the five heterogeneous species appear to show a continuity of variations from the P. bengalensis group to the P. propensalata group, it seems justified to divide the old "Aegaeon" (sensu DE MAN, 1920) into at least three genera and revive Parapontocaris as a full genus.

There is much overlap in the characters used by CHACE (1984) to distinguish the 6 species of this genus. Nevertheless, the abundant material in the present study shows that they are all good species and the sculpturing of the abdominal tergites III and IV shows reliable differences separating them. The range of this rather large genus is also greatly extended in the Indo-West Pacific.

# Key to the species of the genus Parapontocaris

Lateral ridges present on posterior half of abdominal tergite III
2. Dorsal carina of carapace armed with 4 teeth P. caribbaea — Dorsal carina of carapace armed with 5 teeth
<ul> <li>3. Lateral carapacial carinae III usually at least with one side having more than 2 teeth and abdominal somite VI generally armed with more than 2 dorsolateral spines; oblique ridge usually present on posterior part of abdominal pleuron V</li></ul>
<ul> <li>4. Lateral carapacial carinae II armed with 5 or more teeth P. andamanensis</li> <li>— Lateral carapacial carinae II armed with less than 5 teeth</li></ul>
<ul> <li>5. Size small (less than 11 mm cl and with smallest ovigerous female only 6.1 mm cl); abdominal somite II usually armed with 1 dorsal tooth and lateral ridges on abdominal tergite IV generally absent or rudimentary P. bengalensis</li> <li>— Size larger (up to more than 20 mm cl and with smallest ovigerous female 10.1 mm cl); abdominal somite II generally armed with 2 or more dorsal teeth and abdominal tergite IV usually bearing distinct lateral ridges</li></ul>

# Parapontocaris caribbaea (Boone, 1927)

Aegeon caribbaeus Boone, 1927 : 125, fig. 28 (type-locality : Caribbean Sea). Pontocaris caribbaea - DARDEAU & HEARD, 1983 : 10, figs 2f, 3. Pontocaris sp. - TAKEDA, 1983 : 71, fig. 71.

Parapontocaris caribbaea - CHACE, 1984 : 30.

Not Pontocaris caribbaeus - PEQUEGNAT, 1970 : 111 [= P. levigata (Dardeau & Heard, 1983)].

MATERIAL EXAMINED. — Caribbean Sea. "Blake", 1878-1879 : stn 273, 382 m : 1 & 11.6 mm (MNHN-Na 5284).

"Oregon" : stn 1871, Honduras, off Mosquito Bank, 16°39'N, 82°26'W, 457 m, 22.8.1957 : 2 9 17.3 and 19.0 mm, DARDEAU det. (USNM 181353).

Bahamas. "Oregon" : stn 1344, Santaren Channel, off Great Bahama Bank, 22°5'N, 78°8'W, 366-411 m, 16.7.1955 : 2 9 11 and 12 mm, DARDEAU det. (USNM 181352).

DIAGNOSIS. — Body rather robust and pubescent. Rostrum rather short and broad, 0.15-0.17 carapacial length and 0.86-0.97 times as long as broad; somewhat horizontal; lateral teeth more or less at same level as anteriormost dorsal tooth of carapace. Carapace 1.44-1.54 times as long as wide; dorsal carina armed with four teeth; lateral carina I also with four teeth; lateral carina II bearing three teeth; and lateral carina III having 2-3 teeth posterior to branchiostegal spine. Abdominal tergite III with lateral oblique ridges distinct on both anterior and posterior parts. Well-developed lateral ridges also present on abdominal tergite IV. Abdominal pleuron V provided with posterobasal ridge. Abdominal somite II bearing two dorsal teeth while somite VI has one pair of dorsolateral spines.

COLORATION. — A not very clear color photograph of this species was provided by TAKEDA (1983, referred to as "*Pontocaris* sp."). The body appears to be yellowish and the mid-carapace is covered with a broad pale transverse band. The tail fan is banded with white and with the distal part reddish.

SIZE. — Largest male cl 13 mm and largest female cl 19 mm, ovigerous female cl 12 mm (from DARDEAU & HEARD, 1983).

DISTRIBUTION. — Western Atlantic, from the Bahama Islands, Straits of Florida, Gulf of Mexico, and the Caribbean Sea to off Surinam and French Guiana. At depths of 311-885 m.

REMARKS. — P. caribbaea is unique in the genus by having only four dorsal teeth on the carapace. The rostrum of this species is also relatively broader than those of the other species of the genus. The "Pontocaris sp." reported by TAKEDA (1983) from Surinam and French Guiana actually belongs to Parapontocaris and very probably represents the present species, since it has four dorsal teeth on the carapace. On the other hand, the material reported by PEQUEGNAT (1970) from the Gulf of Mexico has five dorsal teeth on the carapace and therefore should belong to P. vicina instead of P. caribbaea.

### Parapontocaris aspera Chace, 1984

Parapontocaris aspera Chace, 1984 : 30, figs 9-11 (type-locality : the Philippines).

MATERIAL EXAMINED. — Philippines. "Albatross" : stn 5459, 13°10'21"N, 123°59'54"E, 368 m, 8.6.1909 : 1 & 17.5 mm (holotype, USNM 205025).

MUSORSTOM 1 : stn 11, 13°59.8'N, 120°21.5'E, 217-230 m, 20.3.1976 : 3 & 16.2-17.8 mm; 2 ovig.  $\Im$  18.8 and 22.2 mm; 12  $\Im$  13.0-21.9 mm (MNHN-Na 5312, 5960). — Stn 40, 13°57.4'N, 120°27.8'E, 265-287 m, 24.3.1976 : 2 & 16.9 and 17.1 mm; 1 ovig.  $\Im$  19.1 mm; 2  $\Im$  11.6 and 11.9 mm (MNHN-Na 5327).

MUSORSTOM 2 : stn 74, 13°53.2'N, 120°26.2'E, 300-370 m, 30.11.1980 : 1 ♀ 21.3 mm (MNHN-Na 5961). — Stn 83, 13°55.2'N, 120°30.5'E, 318-320 m, 2.12.1980 : 6 ♂ 14.7-17.3 mm; 3 ovig. ♀ 19.7-20.7 mm; 5 ♀ 9.1-22.0 mm (MNHN-Na 5959).

Indonesia (Makassar Strait). CORINDON 2 : stn 271, 1°57.8'S, 119°15.0'E, 215-252 m, 7.11.1980 : 1 ♂ 10.5 mm; 2 ovig. ♀ 20.0 and 21.8 mm; 1 ♀ 19.0 mm (MNHN).

**New Caledonia**. MUSORSTOM 4 : stn 246, 22°8.5'S, 167°11.5'E, 410-420 m, 3.10.1985 : 1 ♀ 11.3 mm (MNHN). LAGON, : stn 1062, 20°14.9'S, 163°53'E, 300-320 m, 5.5.1988 : 3 ♀ 11.9-17.9 mm (MNHN). HALIPRO 1 : stn 864, 21°29.004'S, 166°19.113'E, 430 m, 22.3.1994 : 1 ♂ 18.0 mm (MNHN). **Taiwan**. Tai-Shi, I-Lan County, northeastern Taiwan, fish market, commercial trawlers, about 300 m, 16.4.1988 : 2 & 14.5 and 16.7 mm; 2  $\Im$  12.5 and 13.1 mm (NTOU); 3 & 12.4-19.3 mm; 1 ovig.  $\Im$  20.4 mm (MNHN, NTOU in exchange). — 1.9.1989 : 1  $\Im$  16.6 mm (MNHN, NTOU in exchange). — 20.7.1990 : 1  $\Im$  21.6 mm (MNHN, NTOU in exchange). — 27.5.1992 : 1 ovig.  $\Im$  21.3 mm (MNHN, NTOU in exchange). — 15.4.1993 : 2 ovig.  $\Im$  20.5-21.2 mm (NTOU).

Sou-Aou, I-Lan County, northeastern Taiwan, fish market, commercial trawlers, about 300 m, 20.4.1985 : 1 9 15.9 mm (MNHN, NTOU in exchange). — 19.6.1991 : 3 ovig. 9 18.0-19.7 mm (NTOU).

Tong-Kong, Ping-Tong County, southwestern Taiwan, fish market, commercial trawlers, about 300 m, 7.1975 : 1 ♂ 17.1 mm; 1 ovig. ♀ 19.1 mm (MNHN, NTOU in exchange). — 31.10.1984 : 4 ♀ 18.4-19.6 mm (MNHN, NTOU in exchange). — 3.3.1991 : 6 ♂ 13.3-19.8 mm; 8 ovig. ♀ 16.6-22.1 mm; 5 ♀ 8.9-19.6 mm (MNHN, NTOU in exchange). — 2.4.1992 : 1 ♂ 18.7 mm (MNHN, NTOU in exchange).

**Madagascar**. "Vauban" : stn 9, 12°42'S, 48°13.5'E, 455-460 m, 14.4.1971 : 1 spec. 12.8 mm (MNHN). — Stn 31, 12°34'S, 48°15'E, 395 m, 13.9.1972 : 6 spec. 9.5-12.1 mm (MNHN). — Stn 43, 15°24.5'S, 46°2'E, 250-265 m, 7.11.1972 : 1 spec. 7.1 mm (MNHN). — Stn 46, 15°19.1'S, 46°11.8'E, 400 m, 7.11.1972 : 6 spec. 11.6-18.2 mm (MNHN). — Stn 50, 15°19'S, 46°11.8'E, 405 m, 8.11.1972 : 2 spec. 12.2-13.5 mm (MNHN). — Stn 56, 23°36'S, 43°31.6'E, 395-410 m, 26.2.1973 : 5 spec. 11.1-18.4 mm (MNHN). — Stn 61, 23°36.1'S, 43°31'E, 445-455 m, 27.2.1973 : 5 spec. 19.5-24.4 mm (MNHN). — Stn 62, 23°36.1'S, 43°32'E, 340-360 m, 27.2.1973 : 5 spec. 13.8-20.8 mm (MNHN). — Stn 66, 23°36.4'S, 43°31.1'E, 450-460 m, 29.2.1973 : 4 spec. 15.5-20.0 mm (MNHN). — Stn 96, 22°21.3'S 43°3.7'E, 480-500 m, 27.11.1973 : 6 spec. 17.7-23.1 mm (MNHN).

"Mascareignes III" : stn 2, 22°27.9'S, 43°06.7'E, 400 m, 20.12.1985 : 10 spec. 13.6-21.5 mm (MNHN-Na 9718). — Stn 4, 22°19.2'S, 43°06.8'S, 400-410 m, 21.12.1985 : 4 spec. 16.3-19.8 mm (MNHN-Na 9719). — Stn 6, 22°17.3'S, 43°04.3'E, 425-450 m, 21.12.1985 : 6 spec. 18.3-23.5 mm (MNHN Na-9720). — Stn 8, 22°16.7'S, 43°03.9'E, 425-450 m, 22.12.1985 : 2 spec. 14.4-20.8 mm (MNHN-Na 9717). — Stn 10, 22°29.5'S, 43°06.9'E, 450 m, 22.12.1985 : 2 spec. 21.3-21.7 mm (MNHN-Na 9716). — Stn 15, 22°25.2'S, 43°05'E, 425-460 m, 1.1.1986 : 1 spec. 17.5 mm (MNHN-Na 9710). — Stn 19, 22°18.7'S, 43°04.5'E, 400 m, 7.1.1986 : 1 spec. 19.8 mm (MNHN-Na 9707). — Stn 28, 22°23.1'S, 43°04.8'E, 450 m, 15.1.1986 : 1 spec. 19.1 mm (MNHN-Na 9709). — Stn 32, 22°25.8'S, 43°04.3'E, 450-475 m, 19.1.1986 : 1 spec. 21.5 mm (MNHN-Na 9708). — Stn 37, 22°18.2'S, 43°04.8'E, 450-475 m, 21.1.1986 : 1 spec. 23.2 mm (MNHN-Na 9715). — Stn 40, 22°15.9'S, 43°05.2'E, 390-460 m, 22.1.1986 : 1 spec. 17.6 mm (MNHN-Na 9713). — Stn 41, 22°15.8'S, 43°05.7'E, 360-415 m, 22.1.1986 : 2 spec. 14.9 and 21.2 mm (MNHN-Na 9714). — Stn 42, 22°16.7'S, 43°04.9'E, 395-425 m, 22.1.1986 : 1 spec. 22.8 mm (MNHN-Na 9711). — Stn 44, 22°19.5'S, 43°04.4'E, 415-440 m, 23.1.1986 : 2 spec. 18.1 and 18.5 mm (MNHN-Na 9712). — Stn 57, 22°26'S, 43°5.8'E, 460 m, 17.10.1986 : 2 spec. 20.7 and 21.0 mm (MNHN). — Stn 58, 22°26.3'S, 43°05.5'E, 440 m, 17.10.1986 : 1 spec. 21.0 mm (MNHN). — Stn 81, 22°22.8'S, 43°03.3'E, 525 m, 25.10.1986 : 1 spec. 24.0 mm (MNHN). — Stn 117, 22°15'S, 43°06.5'E, 370 m, 28.11.1986 : 2 spec. 13.4 and 16.1 mm (MNHN).

"FAO 60" : stn 73/65, 15°18'S, 46°15'E, 400-450 m, 23.6.1973 : 1 spec. 16.3 mm (MNHN).

DIAGNOSIS. — Body rather robust and distinctly pubescent. Rostrum short and broad, about 0.17 (0.13-0.21) carapacial length and 1.26 (1.01-1.53) times as long as broad; somewhat horizontal; and with lateral teeth more or less on same level as anteriormost dorsal tooth of carapace. Carapace about 1.47 (1.33-1.81) times as long as wide, dorsal carina armed with five teeth, lateral carina I having four teeth, lateral carina II 3-8 (mostly 3-5) teeth and lateral carina III 1-9 (mostly 2-6) teeth posterior to branchiostegal spine. Abdominal tergites III and IV bearing distinct lateral oblique ridges, with those on tergite III further separated into anterior and posterior pairs. Abdominal somite II bearing 2-3 (mostly 2) dorsal spines and denticles, while somite VI is armed with 2-9 (mostly 4-6) dorsolateral spines. Posterior part of abdominal pleuron V having short, oblique ridge. Eggs numerous and small, diameter 0.4-0.6 mm.

COLORATION. — Body, including antennal flagella, brownish-yellow to red-brown (more often). Ridges and carinae on body reddish-brown. Eyes dark brown. Anteromesial part of scaphocerite whitish. Eggs pale yellow.

SIZE. — Largest male cl 19.8 mm and largest female cl 24.4 mm. Smallest ovigerous female cl 16.6 mm in the present study (cl 13.1 mm in CHACE, 1984).

DISTRIBUTION. — Indo-West Pacific from Taiwan to the Philippines, Indonesia, New Caledonia and Madagascar. At depths of 215-525 m.

REMARKS. — When describing the present species, CHACE (1984) mainly used the dentition of the lateral carapacial carina III to separate it from the other species of the genus. However, there are large variations in this character. Of the 172 specimens identified as *P. aspera* in this study, 31 (18%) have both sides, and 12 others (7%) have one side of the lateral carapacial carinae III armed with less than four teeth. Nevertheless, the present study shows that *P. aspera* can be readily separated from the other Indo-West Pacific species of the genus by the body being distinctly pubescent and the posterior half of the abdominal tergite III bearing a pair of distinct lateral oblique ridges (see CHACE, 1984, fig. 9). *P. aspera* is also larger and its body is generally more robust.

On the other hand, the present species shows more resemblances with *P. vicina* from the Atlantic. Other than the rostrum appearing to be longer and more elevated, the body of *P. vicina* is less pubescent and generally has fewer teeth on the lateral carapace and the abdominal somite VI. Although 9.3% (16/172) of the *P. aspera* specimens have both sides of lateral carapacial carinae III bearing less than three teeth while 7.6% (13/170) have abdominal somite VI armed with one pair of dorsolateral spines, both of these situations occur together only in four specimens (2.3%; n = 172). Furthermore, the posterior part of abdominal pleuron V is usually provided with an oblique ridge in *P. aspera* (see CHACE, 1984, fig. 9) but only a weak tubercle is present on the same area in *P. vicina*. Perhaps more material from the western Atlantic is needed to determine which characters are more reliable in separating these two species.

As in CHACE's (1984) "Albatross" material, one aberrant specimen of this study has 6 dorsal teeth on the carapace. Moreover, very rarely there may be three (in three specimens) or five (in one specimen) instead of the regular four teeth on lateral carina I on one side of the carapace.

### Parapontocaris vicina (Dardeau & Heard, 1983)

Pontocaris caribbaeus - PEQUEGNAT, 1970 : 111. Non Boone, 1927. Pontocaris vicina Dardeau & Heard, 1983 : 10, figs 2g, 4-7 (type-locality : Straits of Florida). Parapontocaris vicina - CHACE, 1984 : 30.

MATERIAL EXAMINED. — Straits of Florida. "Bellows" : stn 8, trawl, 23°35'N, 80°22'W, 457 m 15.5.1978 : 1 ovig. ♀ 19 mm (holotype); 1 ♀ 20.2 mm (paratype, USNM 189144).

DIAGNOSIS. — Body rather robust and moderately pubescent. Rostrum relatively long and elevated, 0.22 carapacial length and 1.45 times as long as broad, with lateral teeth distinctly higher than anteriormost dorsal tooth of carapace. Carapace 1.49 times as long as wide, dorsal carina armed with five teeth, lateral carina I having four teeth, lateral carina II bearing three teeth and lateral carina III having 1-2 teeth posterior to branchiostegal spine. Abdominal tergite III with distinct lateral oblique ridges on both anterior and posterior parts. Abdominal tergite IV also bearing well-developed lateral ridges but only weak tubercle present on posterior part of abdominal pleuron V. Abdominal somite II armed with three dorsal teeth and denticles, somite VI bearing one pair of dorsolateral spines.

COLORATION. - Not known.

SIZE. — Largest female cl 21 mm (ovigerous), only male known cl 16 mm, smallest ovigerous female cl 17.5 mm (DARDEAU & HEARD, 1983).

DISTRIBUTION. — Western Atlantic, from the Straits of Florida to the Gulf of Mexico and the Caribbean. At depths of 366-612 m.

REMARKS. — Although *P. vicina* shows some resemblances with *P. aspera* from the Indo-West-Pacific, this Atlantic species generally has the lateral carapace and the abdominal somite VI less spiny (see "Remarks" under *P. aspera* "Remarks").

## Parapontocaris andamanensis (Wood-Mason & Alcock, 1891)

Crangon andamanensis Wood-Mason & Alcock, 1891 : 360 (type-locality : Andaman Sea). — ALCOCK & ANDERSON, 1895 : pl. 9 figs 2-2a.

Pontophilus andamanensis - ORTMANN, 1895 : 184. Aegeon (Parapontocaris) andamanense - ALCOCK, 1901 : 121. Aegeon andamanense - KEMP, 1916 : 379. Aegeon andamanensis - DE MAN, 1920 : 294. Parapontocaris andamanensis - CHACE, 1984 : 30. Not Aegeon (Parapontocaris) andamanense - BALSS, 1925 : 296 (80). (? = P. levigata Chace, 1984).

MATERIAL EXAMINED. — Andaman Sea. "Investigator" : stn 115, 11°31'40"N, 92°46'40"E, 344-403 m, 9.12.1890 : 1 & 12.9 mm (syntype, MNHN-Na 1171).

DIAGNOSIS. — Body naked and slender. Rostrum relatively long and narrow, 0.21 carapacial length and 1.79 times as long as broad, somewhat horizontal and with lateral teeth on same level as anteriormost dorsal tooth of carapace. Carapace 1.77 times as long as wide, dorsal carina armed with five teeth, lateral carina I also having five teeth, lateral carina II bearing 5-6 teeth and lateral carina III having 2-3 teeth posterior to branchiostegal spine. Abdominal tergite III with only anterior part having distinct lateral ridges. Abdominal tergite IV bearing well-developed lateral ridges but posterior part of abdominal pleuron V without ridge. Abdominal somite II armed with two, subequal, dorsal teeth; somite VI having four pairs of dorsolateral spines.

COLORATION. — Described by WOOD-MASON and ALCOCK (1891) and ALCOCK (1901) as chalky-yellow with eyes dark chocolate-brown.

SIZE. — Largest female cl 20 mm and largest male cl 18 mm (including rostrum, from WOOD-MASON and ALCOCK, 1891).

DISTRIBUTION. — Indian Ocean, but only known with certainty from the type-locality in the Andaman Sea, at depths of 344-403 m.

REMARKS. — The male from the Muséum national d'Histoire naturelle probably belongs to the type series of WOOD-MASON and ALCOCK (1891). This Andaman Sea specimen is distinct from the other Indo-West-Pacific species of the genus, except *P. aspera*, in having many more teeth on the lateral carapacial carina II. On the other hand, the absence of lateral ridges on the posterior part of abdominal tergite III readily separates it from *P. aspera*. Although ALCOCK (1901) stated that there are four teeth on lateral carapacial carina I in this species, the specimen recorded herein from the Andaman Sea, as well as the figure of ALCOCK and ANDERSON (1895), shows five teeth on this carina. More material from the Andaman Sea will be useful to fully understand the characteristics of this species. The specimens from Zanzibar reported by BALSS (1925) definitely do not belong to the present species, since they all have less than five teeth on the lateral carapacial carina II. Amongst the other species of the genus in the Indo-West Pacific, the characteristics of the Zanzibar material appear to better agree with *P. levigata*.

Parapontocaris bengalensis (Wood-Mason & Alcock, 1891)

Crangon bengalensis Wood-Mason & Alcock, 1891 : 360 (type-locality : Bay of Bengal). — ALCOCK & ANDERSON, 1894 : 152; 1895 : pl. 9 figs 1-1a.

Pontophilus bengalensis - ORTMANN, 1895 : 184.

Aegeon (Parapontocaris) bengalense - ALCOCK, 1901: 122. - KEMP & SEWELL, 1912: 22.

Aegeon bengalense - KEMP, 1916 : 379.

Aegeon bengalensis - DE MAN, 1920 : 294.

Parapontocaris bengalensis - CHACE, 1984 : 30.

Not Aegeon bengalense - CALMAN, 1939 : 221 (? = P. levigata Chace, 1984).

MATERIAL EXAMINED. — Bay of Bengal. "Investigator" : stn 279, 11°35.15'N, 80°2.15'E, 549 m, 8.3.1901 : 1  $\delta$  8.9 mm; 1  $\Im$  10.1 mm, Reg. no. 4084-5/10, (part of the material in KEMP & SEWELL, 1912, but with different labeled date, 18.3.1911 in KEMP & SEWELL, 1912, MNHN-Na 4714).

**Gulf of Aden** (Off Yemen). "*Meteor*", cruise 5 : stn 267, 13°27.5'N, 47°20.5'E, 359-362 m, beamtrawl, 31.3.1987 : 107  $\Im$  6.4-8.0 mm; 63 ovig.  $\Im$  6.8-10.1 mm; 69  $\Im$  6.1-10.5 mm (SMF). — Stn 287, 12°16'N, 44°8.5'E, 472-479 m, 16.3.1987 : 2 ovig.  $\Im$  5.9 and 6.2 mm; 4  $\Im$  7.3-9.9 mm (SMF).

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DIAGNOSIS. — Body naked and slender. Rostrum relatively long and elevated, about 0.22 (0.2-0.26) carapacial length and 1.54 (1.34-1.78) times as long as broad, with lateral teeth usually higher than anteriormost dorsal tooth of carapace. Carapace about 1.56 (1.42-1.7) times as long as wide, dorsal carina armed with five teeth, lateral carina I usually bearing five (very rarely 4 or 6) teeth, lateral carina II provided with three teeth and lateral carina III having only one tooth posterior to branchiostegal spine. Lateral ridges absent or rudimentary on abdominal tergites III and IV. Posterior part of abdominal pleuron V without ridges. Abdominal somite II generally having one dorsal tooth and somite VI bearing 2-8 (mostly four) dorsolateral spines. Eggs small and numerous, diameter about 0.45 mm.

COLORATION. - Not known.

SIZE. — Largest male cl 8.9 mm and largest female cl 10.5 mm in the present study (total length 48 mm in KEMP & SEWELL, 1912). Smallest ovigerous female cl 6.1 mm.

DISTRIBUTION. — Indian Ocean but only known with certainty in Bay of Bengal, southwest of India and Gulf of Aden. At depths of 265-813 m.

REMARKS. — Thanks to the examination of two topotypic specimens from the Bay of Bengal and the plentiful material from the Gulf of Aden, the characteristics of this species are now more certain. *P. bengalensis* is the smallest species in the genus and also has the smoothest abdomen. The abdominal sculpturing is rather weak, with the lateral ridges on abdominal tergites III and IV indistinct and often absent (see figures of ALCOCK & ANDERSON, 1895). *P. bengalensis* is also distinguished by the abdominal somite II usually having one dorsal tooth. Of the 247 specimens examined, only 12 (4.9%) have an additional, small, dorsal tooth on this somite. Thus, the specimens from Zanzibar reported by CALMAN (1939) should not be *P. bengalensis*, since they all have two dorsal teeth on abdominal somite II and fewer lateral teeth on the carapace. Of the other species of the genus, CALMAN's (1939) material seems to be most similar to *P. levigata*.

### Parapontocaris levigata Chace, 1984

Parapontocaris levigata Chace, 1984 : 34, figs 12-14 (type-locality : the Philippines). — HOLTHUIS, 1993, fig. 292. ? Aegeon (Parapontocaris) andamanense - BALSS, 1925 : 296 (80). Non Wood-Mason & Alcock, 1891. ? Aegeon bengalense - CALMAN, 1939 : 211. Non Wood-Mason & Alcock, 1891.

MATERIAL EXAMINED. — Philippines. "Albatross" : stn 5113, 13°51'30"N, 120°50'30"E, 291 m, 17.1.1908 : 1 & 12.3 mm (holotype, USNM 205000).

MUSORSTOM 1 : stn 11, 13°59.8'N, 120°21.5'E, 217-230 m, 20.3.1976 : 1 ♀ 20.1 mm (MNHN). — Stn 42, 13°54.1'N, 120°28.6'E, 379-407 m, 24.3.1976 : 1 ♀ 12.1 mm (MNHN-Na 5964). — Stn 50, 13°48.2'N, 120°1.8'E, 415-510 m, 25.3.1976 : 2 ♂ 10.8 and 11.6 mm; 3 ovig. ♀ 14.2-16.1 mm; 5 ♀ 8.5-16.6 mm (MNHN-Na 5313).

MUSORSTOM 2 : stn 15, 13°54.9'N, 120°28.4'Ē, 326-330 m, 21.11.1980 : 1  $\Im$  11.8 mm (MNHN-Na 5965). — Stn 26, 13°48.4'N, 120°49.6'E, 299-320 m, 23.11.1980 : 3  $\Im$  12.5-15.0 mm; 1 ovig.  $\Im$  17.7 mm; 6  $\Im$  13.6-17.9 mm (MNHN-Na 5969). — Stn 40, 13°7.7'N, 122°39.1'E, 280-440 m, 25.11.1980 : 3  $\Im$  10.8-11.8 mm; 1 ovig.  $\Im$  13.7 mm; 1  $\Im$  12.7 mm (MNHN-Na 5963). — Stn 75, 13°50.5'N, 120°29.8'E, 300-330 m, 1.12.1980 : 3  $\Im$  9.8-12.7 mm; 1 ovig.  $\Im$  15.3 mm; 5  $\Im$  13.3-16.6 mm (MNHN-Na 5967). — Stn 78, 13°49.1'N, 120°28'E, 441-550 m, 1.12.1980 : 5  $\Im$  10.0-17.0 mm (MNHN-Na 5968). — Stn 83, 13°55.2'N, 120°30.5'E, 318-320 m, 2.12.1980 : 1  $\Im$  11.1 mm (MNHN-Na 5966).

MUSORSTOM 3 : stn 105, 13°52'N, 120°30'E, 398-417 m, 1.6.1985 : 4 spec. 11.5-16.2 mm (MNHN). — Stn 118, 11°58'N, 121°6'E, 446-448 m, 3.6.1985 : 12 spec. 10.6-17.9 mm (MNHN). — Stn 119, 11°59'N, 121°13'E, 320-337 m, 3.6.1985 : 2 spec. 8.3 and 14.6 mm (MNHN). — Stn 125, 11°57'N, 121°28'E, 388-404 m, 4.6.1985 : 16 spec. 11.1-18.4 mm (MNHN). — Stn 135, 11°58'N, 122°2'E, 486-551 m, 5.6.1985 : 1 spec. 14.5 mm (MNHN).

Indonesia. KARUBAR. Kai Islands : stn CC 10, 5°21'S, 132°30'E, 329-389 m, 23.10.1991 : 1 ♂ 14.7 mm (MNHN). — Stn CP 12, 5°23'S, 132°37'E, 413-436 m, 23.10.1991 : 1 ovig. ♀ 16.6 mm (MNHN). — Stn CP 35, 6°8'S, 132°45'E, 390-502 m, 27.1.1991 : 1 ovig. ♀ 15.7 mm; 2 ♀ 10.8 and 13.3 mm (MNHN).

*Tanimbar Islands* : stn CC 42, 7°53'S, 132°42'E, 350-354 m, 28.10.1991 : 1 ovig. ♀ 16.0 mm (MNHN). — Stn CP 69, 8°42'S, 131°53'E, 356-368 m, 2.11.1991 : 2 ♂ 11.9 and 15.9 mm; 7 ovig. ♀ 15.8-17.6 mm; 6 ♀ 9.5-17.2 mm (MNHN). — Stn CP 77, 8°57'S, 131°27'E, 352-346 m, 3.11.1991 : 1 ♂ 14.8 mm; 7 ovig. ♀ 15.3-18.8 mm; 3 ♀ 13.2-15.3 mm (MNHN). — Stn CP78, 9°6'S, 131°24'E, 284-295 m, 3.11.1991 : 2 ♂ 12.0-13.8 mm; 5 ovig. ♀ 15.2-20.0 mm (MNHN). — Stn CP 83, 9°23'S, 131°E, 285-297 m, 4.11.1991 : 2 ♂ 11.6-11.7 mm; 1 ovig. ♀ 13.5 mm (MNHN).

New Caledonia. MUSORSTOM 4 : stn 242, 22°5.8′S, 167°10.3′E, 500-550 m, 3.10.1985 : 2 ♀ 7.8 and 7.9 mm (MNHN).

**Taiwan**. Tai-Shi, I-Lan County, north-eastern Taiwan, fish market, commercial trawlers, about 300 m, 16.4.1988 : 1 ovig. 15.9 mm (NTOU). — 20.7.1990 : 1 14.4 mm (MNHN, NTOU in exchange).

Sou-Aou, I-Lan County, north-eastern Taiwan, fish market, commercial trawlers, about 300 m, 16.3.1985 : 1 9 12.5 mm (MNHN, NTOU in exchange).

**Madagascar**. "Vauban" : stn 9, 12°42'S, 48°13.5'E, 455-460 m, 14.4.1971 : 1 spec. 8.6 mm (MNHN). — Stn 11, 12°39.8'S, 48°15.2'E, 375-385 m, 14.4.1971 : 1 spec. 7.1 mm (MNHN). — Stn 23, 12°26.2'S, 48°13'E, 600-605 m, 19.1.1972 : 1 spec. 11.5 mm (MNHN). — Stn 31, 12°34'S, 48°15'E, 395 m, 13.9.1972 : 6 spec. 7.9-14.2 mm (MNHN). — Stn 46, 15°19.1'S, 46°11.8'E, 400 m, 7.11.1972 : 1 spec. 10.2 mm (MNHN). — Stn 48, 15°18'S, 46°12.1'E, 480-510 m, 8.11.1972 : 8 spec. 10.5-14.1 mm (MNHN). — Stn 50, 15°19'S, 46°11.8'E, 450 m, 8.11.1972 : 1 spec 10.1 mm (MNHN). — Stn 96, 22°21.3'S, 43°3.7'E, 480-500 m, 27.11.1973 : 7 spec. 13.1-15.7 mm (MNHN).

*"Mascareignes III"*: stn 2, 22°20.5'S, 43°6.1'E, 400 m, 20.12.1985 : 4 spec. 14.3-16.3 mm (MNHN-Na 9702). — Stn 4, 22°19.2'S, 43°6.8'E, 400-410 m, 20.12.1985 : 1 spec. 16.1 mm (MNHN-Na 9703). — Stn 6, 22°17.3'S, 43°4.3'E, 425-450 m, 21.12.1985 : 1 spec. 13.8 mm (MNHN-Na 9704). — Stn 26, 22°19.7'S, 43°4.1'E, 450-600 m, 15.1.1986 : 1 spec. 16.6 mm (MNHN-Na 9705). — Stn 41, 22°15.8'S, 43°5.7'E, 360-415 m, 22.1.1986 : 5 spec. 11.6-16.2 mm (MNHN-Na 9706). — Stn 82, 22°11'S, 43°2.9'E, 520 m, 25.10.1986 : 1 spec. 14.4 mm (MNHN). — Stn 117, 22°15'S, 43°6.5'E, 370 m, 28.11.1986 : 1 spec. 15.0 mm (MNHN).

DIAGNOSIS. — Body slender and almost naked. Rostrum relatively long and elevated, about 0.2 (0.17-0.24) carapacial length and 1.69 (1.33-2.22) times as long as broad, with lateral teeth distinctly higher than anteriormost dorsal tooth of carapace. Carapace about 1.63 (1.46-2.07) times as long as wide, dorsal carina armed with five teeth, lateral carina I generally bearing four (rarely 3 or 5) teeth, lateral carina II having three teeth and lateral carina III with 1-2 (mostly one) teeth posterior to branchiostegal spine. Abdominal tergite III generally with only anterior part having lateral oblique ridges. Abdominal tergite IV usually bearing lateral ridges, but posterior part of abdominal pleuron V without ridge. Abdominal somite II armed with 2-3 (mostly two) dorsal spines and denticles, somite VI having 2-11 (mostly 4-6) dorsolateral spines. Eggs numerous and subspherical, diameter about 0.6 mm.

COLORATION. — Body pale yellowish white and covered with minute brown dots. Eyes dark brown. Anterior end of scaphocerite whitish. Posterior part of uropods red brown.

SIZE. — Largest male cl 15.9 mm and largest female cl 20.1 mm. in the present study (cl 20.1 mm in CHACE, 1984). Smallest ovigerous female cl 10.1 mm.

DISTRIBUTION. — Widely distributed in the Indo-West Pacific from Taiwan to the Philippines, Indonesia, New Caledonia, Madagascar and probably also Zanzibar. At depths of 217-605 m (658 m in Zanzibar).

REMARKS. — P. levigata always seems to occur together with P. aspera. Although the characters, such as the number of teeth on the lateral carapacial carinae and the length of the scaphocerite, used by CHACE (1984) to separate these two species are sometimes variable, they can be readily distinguished from each other by the abdominal sculpturing. The oblique ridges on the posterolateral part of abdominal tergite III and the posterior region of abdominal pleuron V are generally absent (occasionally represented by tubercles) in P. levigata. Only in one of the 166 P. levigata specimens examined is there a pair of weak lateral ridges present on the posterior part of abdominal tergite III. The general appearance of P. levigata is more slender and almost naked, and the rostrum is relatively longer and more elevated than that of P. aspera (particularly in adults). The spines and carinae of P. levigata are also generally longer and sharper, respectively, than those of P. aspera.

The present species, particularly for the specimens from Madagascar, actually shows more resemblances with *P. bengalensis*. The anterior part of abdominal tergite III in the Madagascan material (also in small specimens from the other localities) often has the lateral ridges indistinct or even absent. Furthermore, the lateral ridges on abdominal tergite IV are also rudimentary or wanting in some Madagascan specimens. Other than the size of *P. levigata* being distinctly larger, the relatively fewer teeth at the lateral carapacial carina I and the constantly more dorsal teeth on abdominal somite II can probably separate the present species quite well from *P. bengalensis*. In only one *P. levigata* specimen (0.6%, n = 166) is there only one dorsal tooth present on abdominal somite II.

With respect to the lateral carapacial carinae I, 10.8% (18/166) of the specimens have five teeth on both sides. Other aberrant conditions found in this species are that two specimens have 6 dorsal teeth and another specimen has four dorsal teeth on the carapace, and in one specimen there are four teeth on the lateral carapacial carina II of one side.

The specimens from Zanzibar reported by BALSS (1925) and CALMAN (1939) as "P. andamanensis" and "P. bengalensis" respectively seem to have fewer teeth on the lateral carapace and probably belong to the present species instead.

## **EVOLUTION**

**Morphology.** — The 21 species in the present study appear to show a continuum in the morphological characters. The intermediate position of the species of *Aegaeon* between *Parapontocaris* and *Pontocaris* has long been noticed by many authors (eg. KEMP, 1916; DE MAN, 1920; CHACE, 1984). From *Parapontocaris* to *Pontocaris*, the similarities of the five species of *Aegaeon* to these two genera can probably be arranged in the order : *A. boschii, A. rathbuni, A. orientalis, A. lacazei* and *A. cataphractus*. The degree of development of the hepatic groove in these five species fits well with this order. At first glance it seems that the interruption by the hepatic groove caused the second anterior tooth of the lateral carapacial carina II to move upwards. However, the lateral carina II is likely to have been originally on the same level as the antennal spine as in *Parapontocaris* and *A. cataphractus*. Thus, the development of the hepatic groove actually caused the anteriormost tooth of lateral carina II to move gradually from the level of the antennal spine down to the branchiostegal spine, beginning in *A. rathbuni* (with only the anteriormost tooth moved very slightly downwards, the second anterior tooth without any deviation), more so in *A. orientalis*, and finally becoming level with the branchiostegal spine in *A. lacazei* and *A. cataphractus*. However, the second anterior tooth of lateral carina II is still directed towards the antennal spine, but is compressed by the hepatic groove and finally reduced to a tubercle, as in some *Pontocaris* species.

It appears likely that the enlarged branchiostegal spine in *Pontocaris* resulted from the fusion of this spine with the anteriormost tooth of the lateral carapacial carina III, as suggested by their corresponding positions in *A. lacazei* and *A. cataphractus*. Furthermore, the single tooth on the anterior part of lateral carina II in *A. cataphractus* was later split into two teeth, as in *Pontocaris*. Alternatively there is the possibility that the enlarged branchiostegal spine pushed the anteriormost teeth of lateral carina III, and II backwards (i.e. of the two teeth on the anterior part of lateral carina III in *Pontocaris*, the anterior one originated on lateral carina III, the posterior one on lateral carina II). However, the positions and sizes of these teeth in the species of *Aegaeon* seem to lend more support to the former hypothesis. It is worth noting that the second anterior tooth of the lateral carina III in *Pontocaris* both originated from the anterior teeth of lateral carina III, since no such upward movement is observed in any of the other four *Aegaeon* species. The enlargement of the branchiostegal spine pushed the lateral carina III closer to the ventral carapace and the spine eventually reached the level of the pterygostomian spine. On the other hand, the presence of only one tooth on the anterior part of the second tooth, since the armature and sculpturing on the body of these species are generally less developed.

With respect to the number of spines on the posterior margin of abdominal pleuron V, there are two spines (distal one smaller) in *Parapontocaris*, but only one distal spine or sharp tubercle is present at most in *Pontocaris*. In *A. rathbuni* there are two subequal spines on the posterior margin of abdominal pleuron, while only the posterodistal spine is present in *A. orientalis*, *A. lacazei* and *A. cataphractus*. Only the posterobasal spine is distinct on abdominal pleuron V in the geographically isolated *A. boschii*.

It can be easily assumed that *Parapontocaris* is the oldest of the three genera (see also CHRISTOFFERSEN, 1988). Although crangonids are generally considered to be rather advanced among the carideans (e.g. ORTMANN, 1895), species of *Parapontocaris* still have pointed rostrums and the telsons bearing both dorsolateral and terminal spines. Their slender body, narrow scaphocerite and abdominal sculpturing composed of only ridges and carinae are common to many other carideans. However, species of *Pontocaris* appear to possess many "advanced" characters, even though ORTMANN (1895) considered this genus to be the most primitive in the Crangonidae. Other than the modification of the pereiopods in spawning females, which is probably unique in Caridea, the broadened and hardened body, the interlocked thoracic sternum and carapace, cleft rostrum, wing-like branchiostegal spine, widened scaphocerite, spineless telson and the lobular abdominal sculpturing of *Pontocaris* also differ from most carideans. The presence of distinct median spines on the abdominal sternites, and the ventral margins of the abdominal pleura being even sharper in spawning females of *Pontocaris*, are in contrast to the situation in most, if not all, other carideans. It is reasonable to believe that the above mentioned characteristics of *Pontocaris* are in a rather advance state, as some of them (such as the hard integument, interlocked thoracic sternum and carapace, broadened scaphocerite, enlarged branchiostegal spine, lobular abdominal sculpturing, spiny abdominal pleura and spineless telson) are also present in Glyphocrangonidae, which is generally supposed to be the most advanced caridean family [though CHRISTOFFERSEN (1987, 1988) suggested that the Glyphocrangonidae is older than the Crangonidae].

The characteristics of the species of *Aegaeon* are intermediate between those of *Parapontocaris* and *Pontocaris*. Therefore, there is little hesitation to assume that this genus forms a natural link between the other two genera. The tip of the rostrum is simple in *Parapontocaris* but reduced and finally lost, as shown by the tri- and bifurcate rostrum in the species of *Aegaeon* (see also CHRISTOFFERSEN, 1988). The bifurcate rostrum, however, is gradually fused and becomes pointed again in *Pontocaris*. The fact that there is one *A. lacazei* and one *A. cataphractus* specimen in the present study having the bifurcation of the rostrum weaker and in appearance cleft further supports the above interpretation. Furthermore, the posterior thoracic sternites are slightly expanded laterally in *A. lacazei* and *A. cataphractus*, with the spines on the telson of the latter sometimes being rather obscure. Although still distinct, the median spines on the abdominal sternites in most of the species of *Aegaeon* are often rather small on the posterior somites and may even diminish to tubercles in females.

Within Pontocaris, P. hilarula appears to be more closely related to the genus Aegaeon by the anterior end of the lateral carapacial carina III being quite close to the branchiostegal spine, the branchiostegal spine relatively smaller (sometimes only extending to half of the outer margin of the laterally extended scaphocerite), the lateral sinuous ridges of abdominal tergite III interrupted near the lateral ends, and the telson occasionally having four long terminal setae. The dactylus of pereiopod V is strongly modified in the spawning females of P. hilarula. This suggests that the lengthening of the carpus of pereiopod II in spawning females probably represents a more advanced adaptation than the modification of the dactylus on pereiopod V in Pontocaris, though both kinds of pereiopod modification are found together in the Red Sea species. The cleft rostrum appears to have originated from the bifurcate rostrum of Aegaeon and only later changed back to being entire. This is probably shown in P. sibogae and P. major where the rostrums of the juveniles are mainly cleft but become microscopically cleft or entire in adults. As already mentioned, the reduction to only one tooth on the anterior part of the lateral carapacial carina II as well as the loss of the posteromedian spine on abdominal somite IV, are probably secondary and result from the reduction in the sculpturing of the body. Other than the above, however, little can be concluded at present about the evolutionary relationships amongst the species of Pontocaris. Parapontocaris also poses similar problems, though the fewer teeth on the carapace and fewer ridges at the abdomen probably represent a more ancestral state in this genus.

**Biogeography**. — The abundant material from many localities in the present study enables a rough interpretation of the distribution and evolution of these three, closely-related crangonid genera. The genus *Parapontocaris* has a typical Tethys distribution and, except for *P. andamanicus*, the species are widely distributed (fig. 21). Furthermore, *P. aspera* with *P. levigata* and *P. caribbea* with *P. vicina* always occur together in the Indo-West Pacific and in the Caribbean, respectively. The distribution of *Aegaeon* is the widest amongst the three genera, with all the species widely dispersed (fig. 19). The fact that four of the five species are found in the Indo-West Pacific suggests that this genus originated there and only later spread into the Mediterranean and Atlantic. However, it is possible that *A. cataphractus* evolved in the Atlantic, since not a single specimen of this common Atlantic species has been found in the West Pacific by the many large expeditions in this area (the previous record

from New Zealand is incorrect, see "Remarks" under this species). Furthermore, the rather different pattern of abdominal sculpturing and the unique presence of intermediate tubercles on the carapace in *A. cataphractus* also suggest that it may be phylogenetically isolated. If the above is true, then the *A. lacazei* line would logically have given rise to *Pontocaris* in the Indo-Pacific. On the other hand, the occurrence of *A. boschii* in the southwestern Atlantic probably represents dispersion of the genus from the other side of the Atlantic, instead of a relict of a former Carribean/S. Atlantic distribution, since no other species of the genus is found in the West Atlantic, even though the entire coast of West Africa is populated by *Aegaeon* species. The close resemblance of *A. boschii* with *Parapontocaris* may suggest that the geographical isolation of the former resulted in its being more similar to the common ancestor of *Aegaeon*, which is no longer extant in the Indo-West-Pacific.

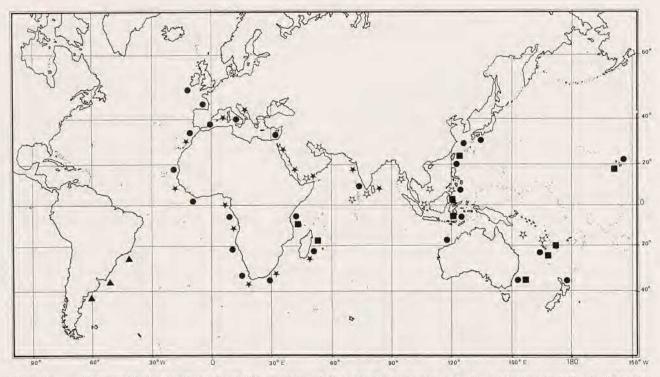


FIG. 19. — Geographical distribution of the species of the genus Aegaeon : ¥, A. cataphractus; ●, A. lacazei;
 ■, A. rathbuni; ≵, A. orientalis; ▲, A. boschii.

Of the 10 species known in *Pontocaris*, 8 are found in the Philippine Indonesian area (fig. 20), three of which apparently have very restricted distributions (i.e. *P. laurentae* occurs only in Makassar, *P. spinifera* in the Flores Sea and *P. major* in the northeastern Philippines). Northwards only two species, namely *P. sibogae* and *P. pennata*, are found in Japan and Taiwan. On the other hand, only three species, *P. propensalata*, *P. sibogae* and *P. hilarula*, have dispersed south to New Caledonia (*P. propensalata* may also occur in southeast Australia). The entire Indian Ocean has only two species, with *P. affinis affinis* found scattered in this region and *P. propensalata* just across the Strait of Malacca into the Andaman Sea, or perhaps Bay of Bengal. In the Red Sea (including the Gulf of Aden), a subspecies of *P. affinis* is found with another endemic species *P. profundior*. The occurrence of both kinds of pereiopod modifications in the spawning females of these two endemic forms further suggests that the Red Sea is a rather distinct zoogeographical subregion. The above distribution pattern matches quite well with EKMAN's (1953) zoogeographical theory that the Indo-Malay region is a species center. Thus, it seems likely that *Pontocaris* originated in the Indo-Malay region in relatively recent times and is still actively evolving.

The Tethys distribution of *Parapontocaris* suggests that it is the most ancient of the three genera. The genus *Aegaeon* probably evolved from a *Parapontocaris* ancestor in the Indo-West Pacific and only later migrated to the Mediterranean and Atlantic. The considerably fewer species but much wider distribution of *Aegaeon* indicate that it

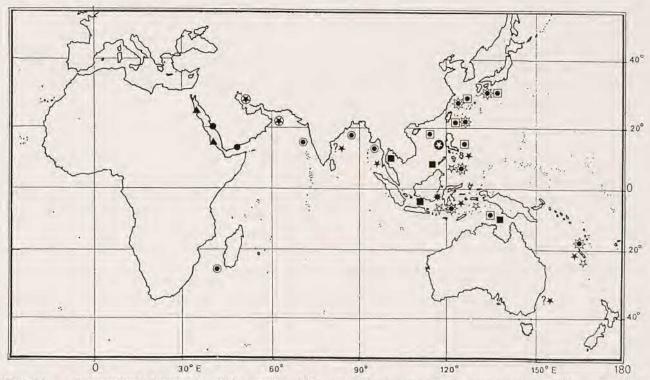


FIG. 20. — Geographical distribution of the species of the genus Pontocaris :¥, P. propensalata; ●, P. profundior;
■, P. arafurae;¥, P. hilarula; ●, P. affinis affinis; ▲, P. affinis allodactylus; ●, P. major; ¥, P. laurentae;
₩, P. sibogae; ■, P. pennata; ★, P. spinifera; ⊕, P. affinis affinis or P. affinis allodactylus; ?, exact identity still uncertain.

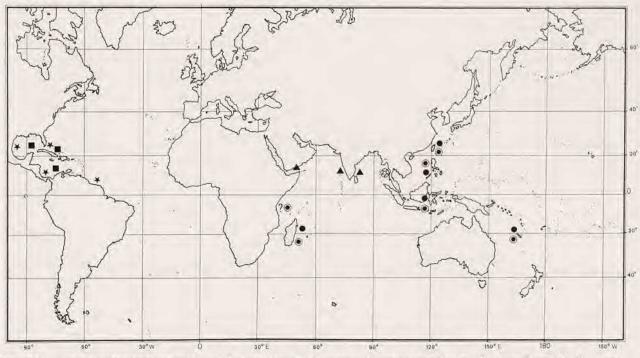


FIG. 21. — Geographical distribution of the species of the genus Parapontocaris :¥, P. caribbaea: ●, P. aspera;
■, P. vicina; ③, P. andamanensis; ▲, P. bengalensis; ●, P. levigata; ?, exact identity still uncertain.

has a longer history than *Pontocaris*. The latter probably originated in the Indo-Malay region and is still actively evolving there.

Both the morphological evidence and the distribution patterns show that the three genera defined in the present study may truly represent "natural" discontinuities. More details on the distribution of the living species and of possible fossils, as well as biochemical or phylogenetic analyses, may perhaps provide more information on the phylogenetic relationships of the species in these three closely related groups.

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